

A REVISION OF THE GENERA *PHASCOLION*
THÉEL, AND *ONCHNESOMA* KOREN AND
DANIELSSEN (SIPUNCULA)

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Abstract.—The two closely related sipunculan genera, *Phascolion* and *Onchnesoma* are reviewed and the species reevaluated in light of a critical examination of historically used morphological characters. Wherever possible, type-material was examined and the accuracy of original descriptions verified. Of the 52 putative species in *Phascolion*, 23 species and two subspecies are retained as valid and are arranged into five subgenera (two new ones: *Villiophora* and *Isomya*). The four *Onchnesoma* species and one subspecies are retained but one new subspecies is added. The known distribution of each species is given and a brief zoogeographical analysis is offered. Keys to all the species are included.

The sipunculan genus *Phascolion* was erected by Théel in 1875 to contain three species. An interesting history of this taxon is presented in Hendrix (1975). In their monograph, which we use as the starting point for this work, Stephen and Edmonds (1972) include 34 species names. Since then 18 new species have been described.¹

In the same year, the closely related genus *Onchnesoma* was created by Koren and Danielssen (1875) for three species which had many of the same character states as *Phascolion*. Their *Onchnesoma* work had already been submitted to the publisher when Théel's *Phascolion* paper was published (see appendix in Koren and Danielssen 1877:152) so at the outset there was no comparison of these two taxa. Also, the characters used by the original authors differed from those used by 20th century writers, especially in not mentioning the single nephridium and actual anal location in the generic diagnoses. Koren and Danielssen's *Onchnesoma* diagnosis read: "Body small, pear-shaped, proboscis long, anal aperture a little in front of the base of proboscis, no tentacles, no vascular system, one retractor." Selenka (1885) contributed to this construct by moving what had been *Phascolosoma squamatum* into *Phascolion* but Théel (1905) moved it on to *Onchnesoma*. Selenka's six reasons for moving *squamatum* helped clarify the issue but as Théel (1905:97) pointed out, Selenka repeated some of Koren and Danielssen's mistakes by looking only at their description, not the worms.

As we worked with these genera, it became increasingly difficult to maintain their separate generic status. The "gap" became less and less clear especially when working with *Phascolion* species lacking hooks and holdfasts and with the retractor muscles fused for most or all of their length. At one point we had concluded that *Onchnesoma* should be ranked at the subgeneric level but have subsequently decided to not propose such a change at this time. They are clearly closely related

¹ The endings of six species names have been changed in this paper to comply with the ICZN. The genus name is neuter and all adjectival species names should be in the neuter form. We are indebted to Dr. G. Steyskal, Washington, D.C. for these corrections.

and data from developmental or biochemical analyses would help resolve this uncertainty.

Stephen and Edmonds (1972) list the two species of *Onchnesoma* found in Théel (1905). An additional two species and one subspecies have been described since then (here we add one new subspecies).

This report is one in a series of efforts to apply the Cartesian methodology of doubt, analysis, synthesis and enumeration to the currently accepted species of sipunculans. The process involves: 1) a familiarization phase that includes an analysis of written descriptions to look for subsets of related species within a subgenus or genus. 2) A comparative study of characters presumed to have taxonomic significance. To determine the extent of variation present within one gene pool, series of individuals of different sizes from relevant populations are studied. During this phase we also look for new characters which may be potentially useful. 3) An examination of type-material and other reference material to validate or correct (if necessary) the original description. 4) With these data we then make decisions about meaningful differences and species validity culminating in a re-definition of the taxa as required. The organization of this report reflects that process addressing first *Phascolion* then *Onchnesoma*. Table 1 lists all species considered with any status changes resulting from this study.

Phascolion Théel, 1875

Type-species.—*Sipunculus strombus* Montagu, 1804.

Diagnosis.—Species with trunks less than 4 cm in length, many inhabiting mollusc shells. Introvert one-half to 4 times trunk length, usually with hooks. Trunk often with chitinized 'holdfast' papillae. Body wall with continuous muscle layers. Oral disk carrying tentacles arranged around mouth, reduced in a few species. Introvert retractor muscle system modified by fusion of dorsal and partial (rarely complete) fusion of ventral pair. Further fusion to form single retractor column may occur. Except in *P. cirratum*, contractile vessel without villi but may be vesicular. Gut with spiral coil and loops or just loose loops. Spindle muscle absent. One nephridium.

Morphological Characters of *Phascolion*

1. *Holdfast or attachment papillae.*—The epidermal papillae in the genus *Phascolion* are large and diverse. Those in the mid region of the trunk (sometimes posterior) may secrete chitinoid material to form hardened structures which are referred to as holdfast or attachment papillae—the name suggesting their function. This assumed function has not been demonstrated but Hylleberg (1975) has observed that they do scrape the bacteria from the inside of the empty shells used for shelter. Perhaps the term cleaning papillae or scrapers would be more descriptive of their structure.

Much of the taxonomic literature treats these as if they were fixed, static and uniform in size, shape and distribution within a species. While some writers have described the variations within populations (Théel 1875a; Wesenberg-Lund 1929), others have ignored these works. It is clear that whatever the genetic potential might be, its expression may be modified by environmental factors such as 1) the physical nature of the shelter (hard, soft, loose or tight fitting (Gerould 1913); 2) the availability of certain chemical elements (e.g., iron, Gibbs 1985), or 3) the

material (sediment, mucus, etc.) deposited on the inside of the shell (Hylleberg 1975). The other variable is the ontogenetic stage, i.e., no member of this genus is known to have chitinized holdfasts in very young juveniles. In populations of *P. strombus* holdfasts are present in 3–4 mm worms, but not yet evident in 1–2 mm worms. Therefore, when one has a 1 or 2 mm worm without chitinized holdfasts, it is very risky to assert that this is the adult condition, unless gametes are also present. However, if the specimen is more than 3 or 4 mm and lacks holdfasts, one can be fairly certain that this represents reality for the adult.

The number, form, and distribution of these holdfasts, when present, are very difficult to describe with confidence. As noted above, several authors have addressed this problem. How much plasticity exists within any one gene pool is yet to be unequivocally determined, but on a single animal (one genotype), the size, degree of pigmentation and shape is so variable that we seriously question its use in species diagnoses except in a very general way. There are three general conditions: 1) a few species exhibit no large glandular papillae in the midsection of the trunk (e.g., *P. lutense*); 2) some have large glandular papillae which appear as flattened spheres but with no solid chitinous deposits around their border (e.g., *P. tuberculosum*); and 3) most species have these papillae and a few to many of them secrete a border of chitin which may be pale brown to black, from 30–300 μm across the base of the chitinized portion, and the shape being some variant of a crescent or U-shape, sometimes appearing with a tooth or spine. Within populations having condition 3 (holdfasts) one must be careful to note that what is seen in a particular individual or series of specimens may not represent all of the phenotypic possibilities for that species.

To use the shape or size of a glandular papilla and its secretory products as an exclusive property is unwise. Rather, these should be considered as examples of what is within the range of possibilities for a particular species with the understanding that in smaller or larger worms living in a different microhabitat these parameters may vary. In other words, the number, type, and size varies among subsets so that while the genetic potential for producing these units exists, environmental factors modify their expression (Gibbs 1977). Figures 1 and 2 show some of the variety in a series of holdfast papillae present in this genus.

2. *Introvert retractor muscles*.—In larval *Phascolion* there are two pairs of introvert retractor muscles, the primitive, plesiomorphic condition in the phylum (Åkesson 1958). Very early in their ontogeny each pair (dorsal and ventral) fuse together for most or all of their length giving the appearance of only two muscles, the ventral often with two origins near the posterior end of the trunk (Gerould 1913). In a few species the fusion is more extensive, with the dorsal and ventral set coming together to form a single muscle. A model would be to think of there being three zippers closing from anterior to posterior along these muscles: the one between the dorsal pair almost always closing down all the way, the one between the ventral pair usually remaining unzipped for the last millimeter or so, then the third zipper between this newly formed pair (fused dorsal and fused ventral) usually closing only a short distance (*P. strombus* and *P. tuberculosum*, Fig. 3A, B), sometimes closing about $\frac{1}{2}$ – $\frac{3}{4}$ the distance (*P. lutense*, Fig. 3C) and occasionally closing all the way (*P. cryptum*, Fig. 3D). This latter condition also exists in the genus *Onchnesoma*.

When two muscles are evident, biologists have used certain attributes as diagnostic characters. One which is useful is whether they are of equal or unequal

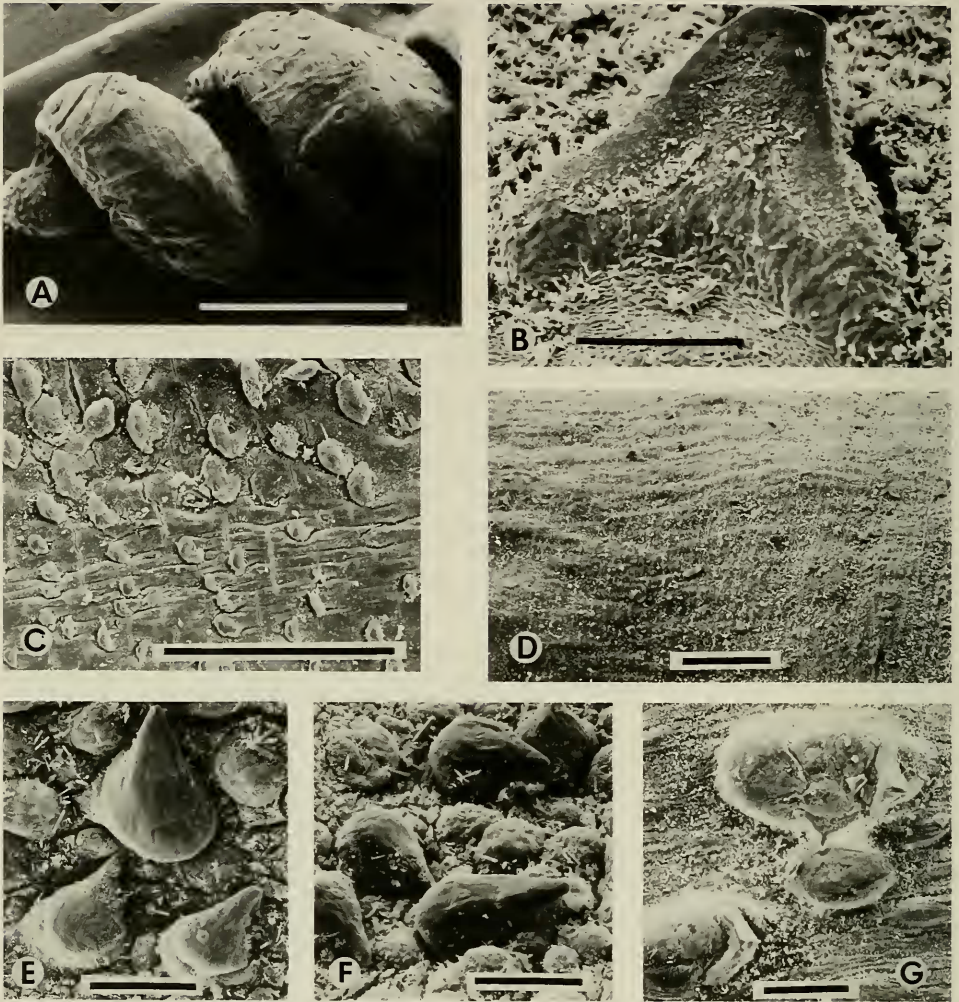


Fig. 1. Scanning electron micrographs of *Phascolion* skin and holdfast papillae: A, *P. strombus* from gastropod shell showing V-shaped holdfasts on upper right coil and epizoans on posterior end (scale line = 1 mm); B, Chitinous holdfast papilla of *P. strombus* (scale line = 20 μ m); C, Ventrolateral section of *P. strombus* showing variety of sizes and shapes of holdfast papillae (scale line = 1 mm); D, Skin of *P. lutense* showing complete absence of holdfast papillae; E, F, *P. caupo*'s large holdfast papillae from two different angles (scale line = 0.1 mm); G, *P. collare* showing 0, 1, and 2 teeth on holdfast papillae (scale line = 0.1 mm).

size. In some species the ventral muscle is slender, the dorsal being 2.5–10 times the thickness of the ventral. This difference is only true for worms exceeding 2 mm in trunk length. In smaller individuals the two muscles are of almost equal size. This ontogenetic series is illustrated in Fig. 4 with *P. strombus* over a range of sizes. In those species with retractors of equal size the dorsal may occasionally be larger (1.3 \times) or slightly smaller (0.7 \times) than the ventral but there is a clear gap between these two groups (when trunk is over 2 mm long).

It is possible to overlook the ventral retractor muscle when it is thin (as in *P.*

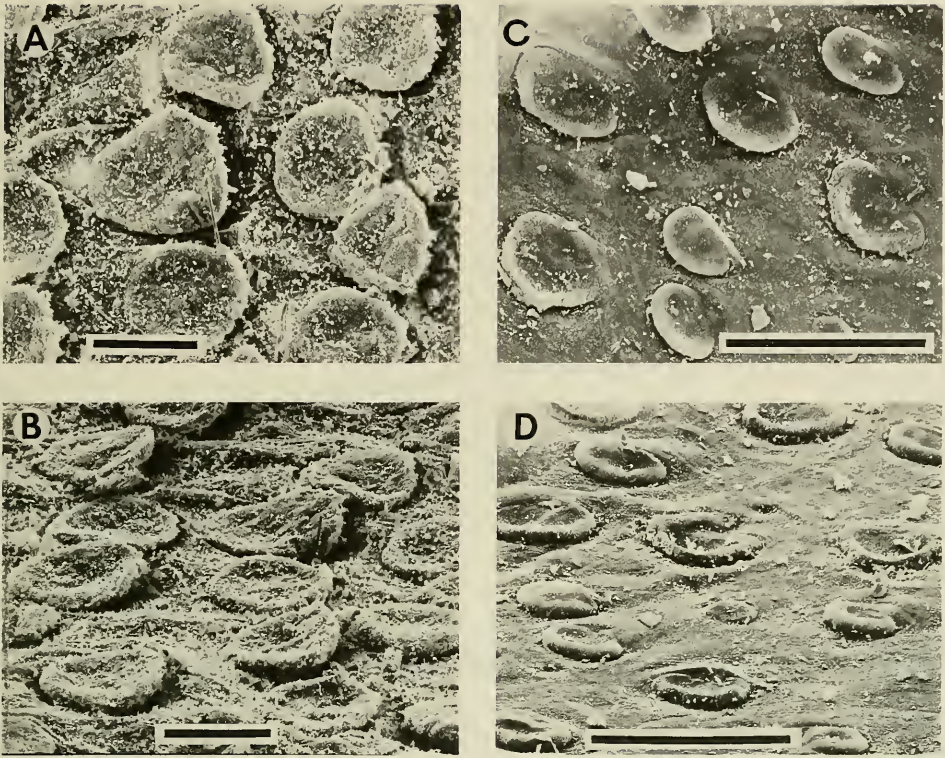


Fig. 2. Scanning electron micrographs of *Phascolion* holdfast papillae at two different angles: A, B, *P. tuberculosis*'s bulbous non-chitinized papillae; C, D, *P. hedraeum*'s papillae with border slightly chitinized. (Scale lines = 200 μm .)

strombus) and conclude that only one muscle is present. This mistake has been made by biologists of current, as well as past eras, especially when the ventral muscle is very thin and has the esophagus attached to and covering a portion of it. This is especially difficult in the contracted state when only 1–2 mm of the muscle is visible at the posterior end. When the coelom is filled with gametes or sediment from a ruptured intestine this is further obscured. It may be more like a spindle or fixing muscle in appearance and can be easily broken when small. Additionally, in species said to have only one muscle but where the esophagus is not shown connected to this muscle, it may be that it is attached to the overlooked and possibly broken ventral retractor.

A less useful attribute is the position of the origins (roots) with respect to one another. It has been claimed that in some species they are at the same anterior/posterior level, while others are described as being at different levels. An examination of this hypothesis suggests it should be abandoned. In 70 specimens from several *P. strombus* Atlantic Ocean populations, when calculated as a percentage of trunk length, this distance ranged from 0–15%, rarely greater than 5%, many being at the same level (0%) especially, but not exclusively, the smallest worms. This species has historically been described as having its retractor origins at different levels. Plainly, this is not consistently true. On the other hand, *P. tu-*

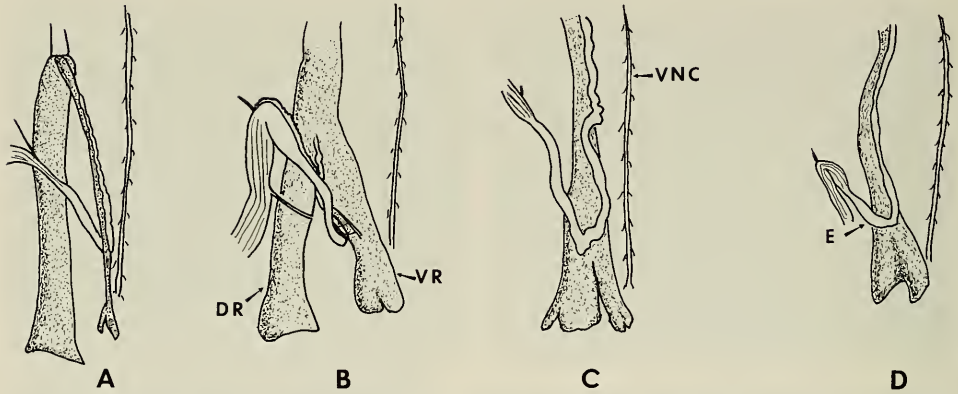


Fig. 3. Schematic drawing of introvert retractor muscles and esophagus in *Phascolion* subgenera: A, *P. (Phascolion)*, ventral muscle considerably thinner than dorsal; B, *P. (Isomya)*, dorsal and ventral muscles approximately equal size; C, *P. (Montuga)*, muscles partly fused with esophagus leaving before any split; D, *P. (Lesenka)* and *P. (Villiophora)*, completely fused retractor column. (DR = dorsal retractor muscle; E = esophagus; VNC = ventral nerve cord; VR = ventral retractor muscle.)

berculosum, with its origins allegedly at the same level, showed a range from 0–13% (most of the 20 specimens being between 1–6%). Similar variations can be found in other species, therefore, this character has little systematic value. A final aspect is the relationship between the origins of the ventral retractor and the ventral nerve cord. Whether the retractors straddle the nerve cord or are to the left of the midline, and whether the origins are anterior, at the level of, or posterior to the end of the nerve cord has been historically considered as constant within a species. Our data do not support this assumption. It is true that in most of the Atlantic *P. strombus* the retractors are slightly posterior (0.1–0.5 mm which is 0.3–4%, a few are up to 8%, of the trunk length) and offset to the left. However, there are a significant number where these points coincide and a few in which the retractors originate anterior to the termination of the ventral nerve cord by 1.5–4%, sometimes to the left and sometimes straddling it. In very small worms this relationship is difficult to ascertain with certainty. The norm in this genus seems to be that the ventral retractor origins are posterior and slightly to the left of the nerve cord, but they occasionally are located anterior and/or on the midline. No correlation with the degree of coiling is apparent. Finally, six of the 70 Atlantic *P. strombus* (9%) showed complete fusion of the ventral retractors so that there was a single origin.

3. *Contractile vessel*.—The tentacular coelom is continuous with a blind tube which is attached to the esophagus and probably functions in gas exchange. This so-called contractile vessel (its contractile capability has not been demonstrated) is thin walled and generally is about one-quarter the diameter of the esophagus. As in other genera (e.g., *Siphonosoma*, Cutler and Cutler, 1982) there is confusion about contractile vessel villi. Contrary to some assertions there is only one species in *Phascolion* which has true villi (*P. cirratum*). What is present in some others are folds or vesicular pouches along some portion of the tube, perhaps due to the relative inelasticity when the adjoining retractor muscle is contracted. The size of this vessel and extent of folding or vesicle formation does seem to be correlated

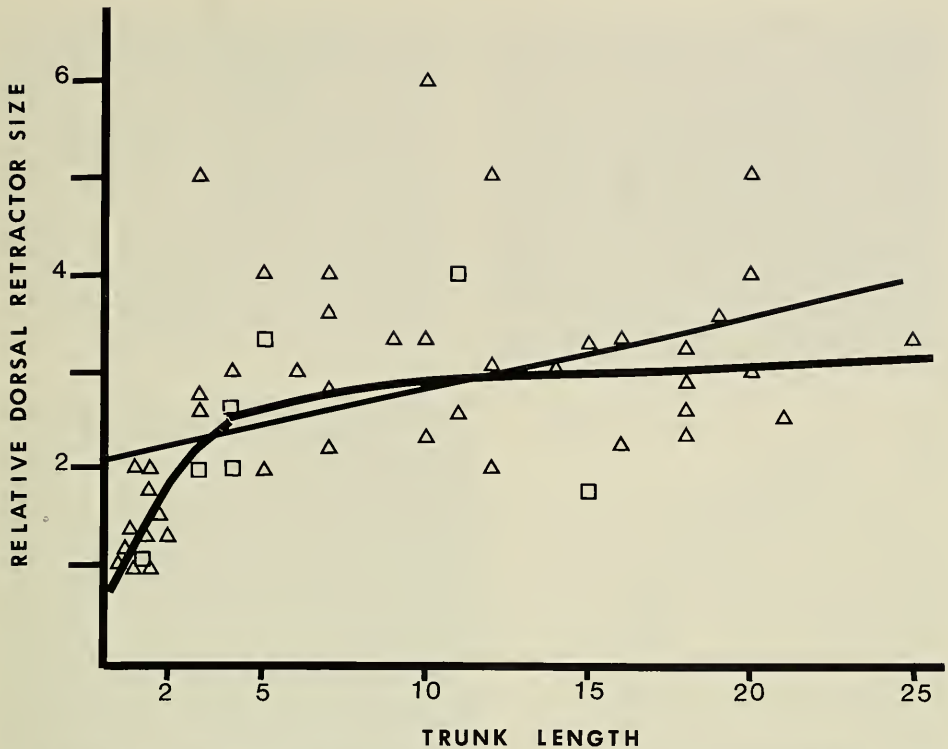


Fig. 4. Relative size of introvert retractor muscles in a population of *P. strombus* ranging in trunk length from 0.6–25 mm. Values on Y axis are the width of dorsal retractor divided by width of ventral retractor muscle. $N = 59$; curve is a hyperbolic function $Y = x/(a + b*x)$, $a = 0.51$, $b = 0.32$ and Index of Determination = 0.69; squares represent 2 individuals. The straight line represents linear regression with a poor fit (Index of Determination = 0.2).

with the number of tentacles. As in *Themiste* and *Thysanocardia*, this is probably an adaptation to low oxygen tension and larger size. *Phascolion cirratum* is known only from the Red Sea where the temperature is high and the oxygen tension is low. It has many tentacles and an elaborate array of villi. We consider this to merit subgeneric rank.

4. *Introvert hooks*.—The presence of scattered hooks on the introvert just behind the tentacles is characteristic of most members of this genus. When an individual is reported as lacking hooks it may be the result of: 1) genotypic change for the species; 2) loss of deciduous hooks as part of ontogeny; 3) delayed replacement during regeneration of lost introvert; 4) oversight on the part of the observer (some hooks are very small and pale and, especially when working with a withdrawn introvert, may be hard to find). When conditions 2, 3, or 4 are operative, it can be misleading and create unnecessary taxonomic confusion.

It is our conclusion that the real condition #1 is uncommon and found in only a few derived forms, all with completely fused retractor muscles (*P. cirratum*, *P. cryptum*, *P. hupferi*, *P. rectum*, *P. valdiviae sumatrense*, and the genus *Onchnesoma* are all without hooks as adults).

Hook morphology has only been used to a minimal degree as a taxonomic

character in *Phascolion*. There are, however, three general types and, while this division is somewhat artificial, it may help with species identification. Type I hooks (size 20–250 μm) have been called “claws” or “spines.” They have pointed non-recurved tips and many have narrow bases. The spines are more perpendicular to the surface of the skin than are the claws. These include *P. bogorovi*, *P. hedraeum*, *P. lutense*, *P. microspheroidis*, *P. pacificum*, *P. strombus*, *P. ushakovi*, and *P. valdiviae*. Type II hooks (size 40–220 μm) are broad-based, heavy, with a recurved pointed tip. They also show an internal light triangle under the light microscope. These are *P. convestitum*, *P. hibridus*, *P. pharetratum*, and *P. tuberculosum*. Type III hooks (size 20–70 μm) are also broad-based and recurved but with a round tip. Included species are *P. abnorme*, *P. caupo*, *P. collare*, *P. lucifugax*, *P. medusae*, *P. megaethi*, and *P. robertsoni*. These types are illustrated in Figs. 5 and 6. When observing hooks on a slide one must be careful to account for distortion caused by the orientation of the hook to the plane of the slide (Fig. 5B).

5. *Intestinal loops and coils.*—The prevailing myth is that most members of this genus lack the usual sipunculan double helix gut coil, this having been replaced by a series of loose loops in all but a few species. *Phascolion strombus* is by far the most commonly collected member of this genus and it often lacks a gut coil. This condition must have been assumed to be common for the genus. A survey of the literature showed this to be in error, only ten putative species have been described as lacking the spiral coil, i.e., less than one-quarter of the described species. Of the 23 remaining valid species, only eight lack the gut coil.

6. *Intestinal fastening muscles.*—In this phylum, there are two different kinds of threadlike muscles used for fastening the intestine in place: the spindle and the fixing muscles. There has been some inconsistency in the application of these terms in this genus. A spindle muscle has its origin either in the body wall just anterior to the anus or on the distal part of the rectum. It extends along the rectum, through the gut coil and either terminates within the coil near the most posterior coil, or extends through the whole spiral and inserts on the posterior tip of the body. Fixing muscles are much shorter and go from the body wall (at a variety of points) to the wall of the esophagus or intestine. These are therefore much shorter, and their numbers (often 2–5) and particular points of origin or insertion seem variable but this is difficult to ascertain with precision due to their small and fragile nature.

In the literature five species are said to have spindle muscles, two of Fischer's (*P. valdiviae* and *P. sumatrense*) and three of Murina's (*P. pacificum*, *P. sandvichi* and *P. ushakovi*). Our inspection of these types showed a strong fixing muscle from the posterior end of the gut coli but no spindle muscle. Most authors use fixing or fastening muscles but in Stephen and Edmonds (1972) there are five species in which the term mesenteries, not muscle is used. This seems to be a matter of the translator's choice because in the same work they say that *P. abnorme* and *P. hupferi* have spindle muscles while in the original the term ‘Befestiger’ is used, not ‘Spindelmuskel,’ so that translation is misleading. Only one species is said to lack any fasteners but for six species no mention is made as to their presence or absence.

We have found no evidence of a true spindle muscle in any of the *Phascolion* material we have examined. Therefore, we conclude that it is absent in the genus; fixing muscles, however, are usually present.

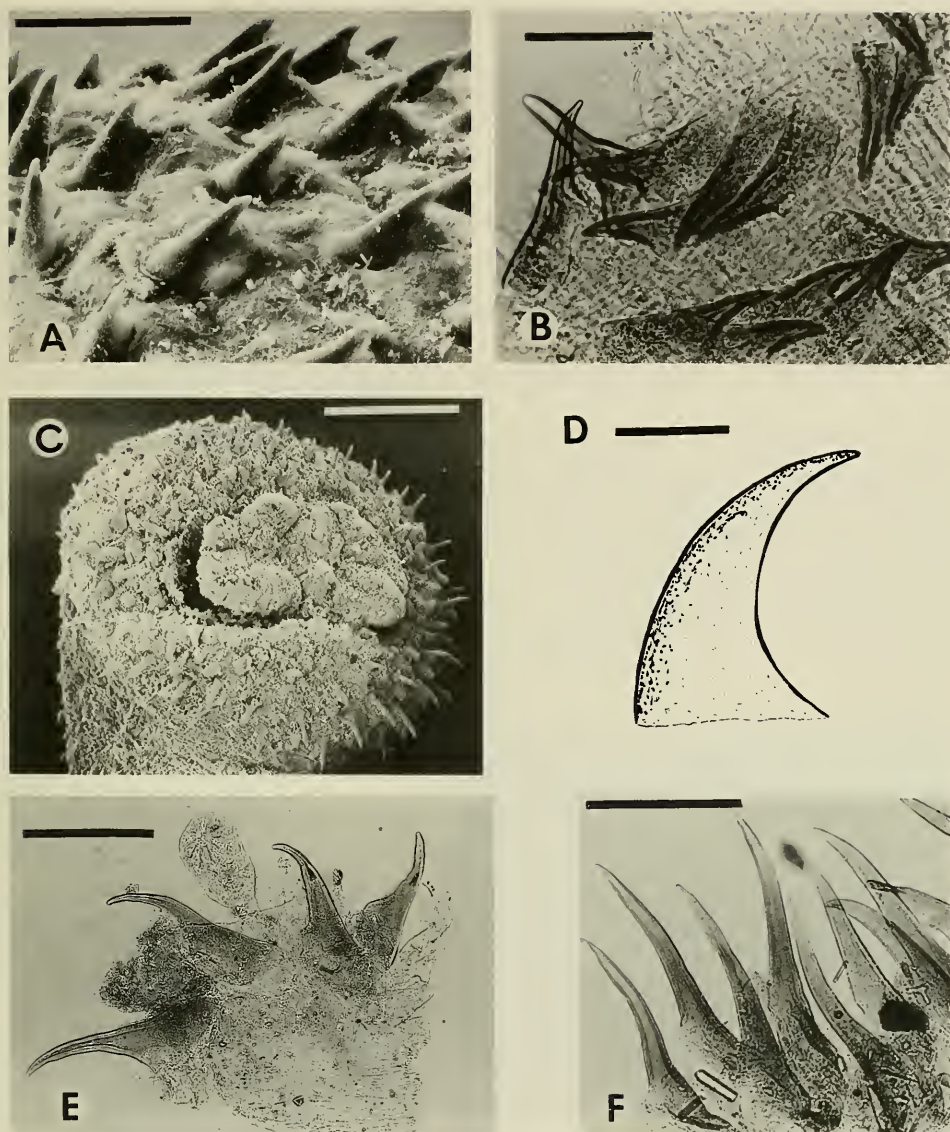


Fig. 5. *Phascolion* introvert hooks (Type I): A, B, *P. strombus* (scale = 100 μ m), B showing how orientation of hook on slide affects appearance; C (scale = 200 μ m), D (scale = 20 μ m), *P. microspheroidis*, C also showing tip of introvert with tentacular lobes; E, *P. bogorovi* (scale = 200 μ m); F, *P. ushakovi* (scale = 200 μ m).

7. *Tentacular crown*.—It is difficult to determine with certainty whether there is a genetically determined upper limit on the number of tentacles in a given species. In other genera this appears to be somewhat indeterminate, the number of tentacles continuing to increase throughout the life of the worm. However, in *Phascolion* there appears to be, if not a fixed number, at least a small range.

In general, one sees four types of tentacular crowns in this genus: 1) no distinct tentacles but only a few (less than 10 lobes) (e.g., *P. lutense*, Fig. 7B). As the production of tentacles occurs after settling of the larvae (Åkesson 1958; Gibbs

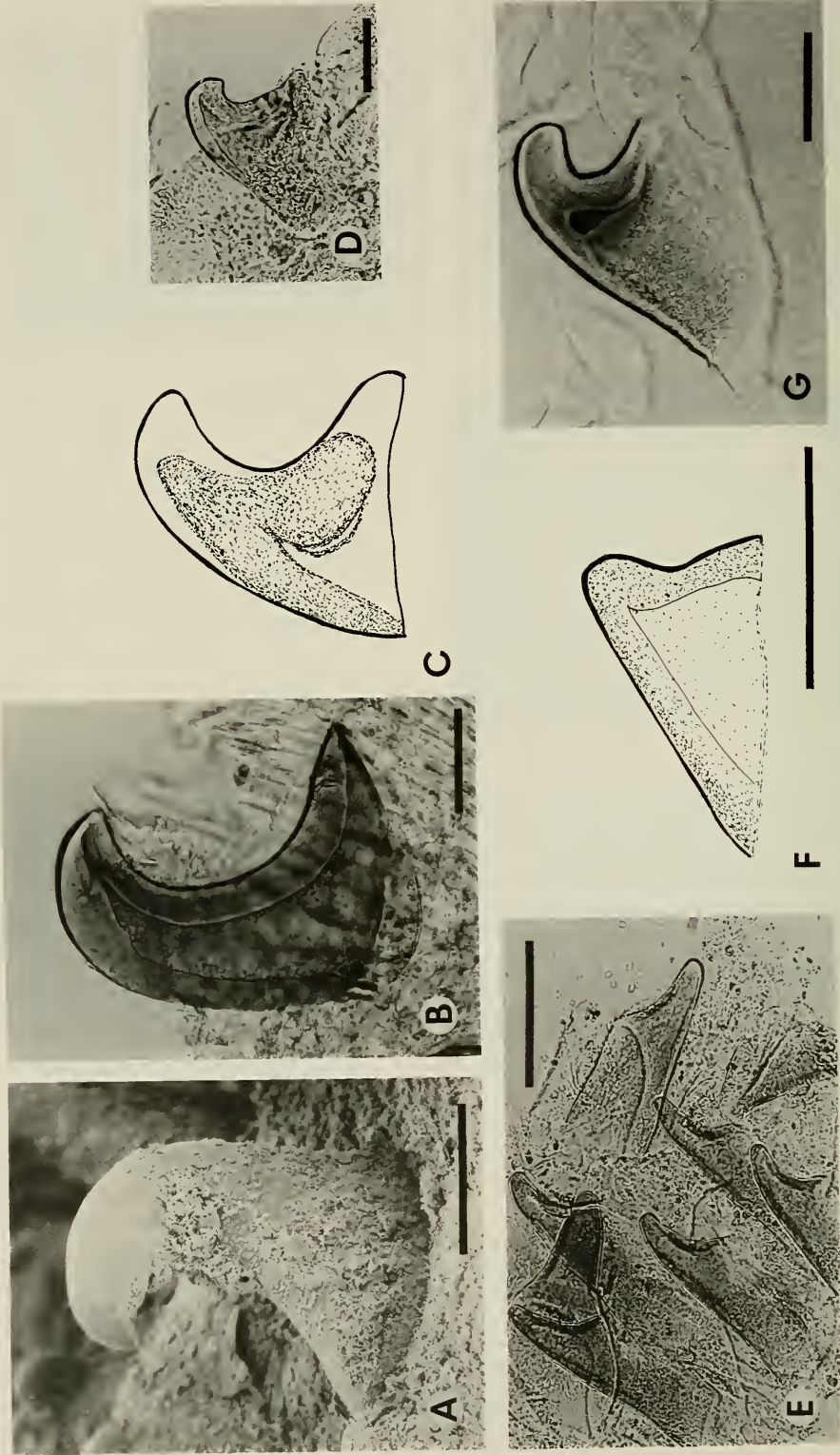


Fig. 6. *Phascolion* introvert hooks (A-D, Type II; E-G, Type III): A, B, SEM and photograph of *P. tuberculosum*; C, *P. pharetratum* (after Sluiter 1902, fig. 3); D, *P. convesitum*; E, *P. medusae*; F, *P. collare*; G, *P. lucifugax*. (Scale lines = 50 μ m.)

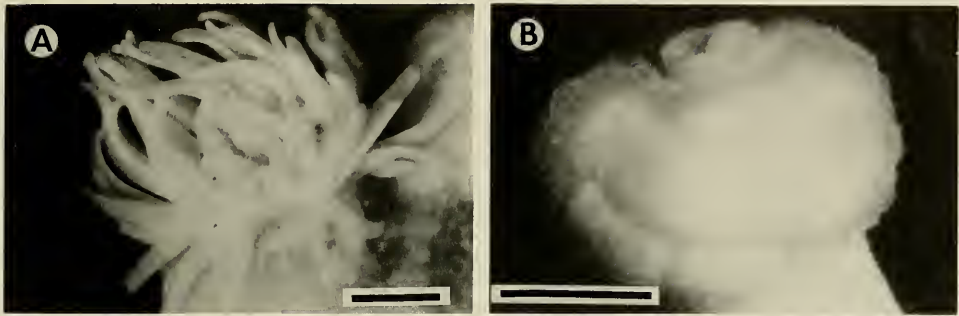


Fig. 7. Distal tip of introvert with tentacles showing the two extreme conditions in *Phascolion*: A, *P. robertsoni* with many tentacles; B, *P. lutense* with reduced lobes. (Scale lines = 0.5 mm.)

1977) the presumed absence of tentacles may sometimes be due to the juvenile condition of the specimen; 2) in adults there are 15–28 well defined tentacles of varying shape but usually broad and digitiform (e.g., *P. strombus* and *P. tuberculosum*; see Théel 1905, pl. VI, figs. 82–86); 3) adults with 40–60 slender, digitiform tentacles (e.g., *P. robertsoni*, Fig. 7A and *P. medusae*); 4) a reduction to the four primary tentacles but each of these branching in a dendritic pattern (*P. cryptum*). This species has “accessory tentacles” on the bulbous area below the tentacles where hooks are commonly found in most species.

It is very difficult to determine this number in small specimens with introverts withdrawn and therefore is of limited taxonomic value. Additionally, tentacle number is not species specific in the sense of being different from all other species or in the sense of each member of the population having exactly the same number. In a broad sense, as part of a suite of characters, tentacle number can be useful to the taxonomist.

8. *Nephridium*. — When species descriptions are constructed authors often make reference to a suite of characters relating to the single nephridium. 1) Position of nephridiopore with respect to the anus is almost always mentioned. For the genus *Phascolion* this is always posterior to the anus. The two stated exceptions are unsupported (see discussions of *P. abnorme* and *P. ikedai*). Whether it is 1 mm or 6 mm posterior does not seem to be a species-specific character but more a factor of size with much individual variation within a population. 2) Size of nephridium is often mentioned (as $\frac{1}{4}$, $\frac{1}{3}$ or $\frac{1}{2}$ the trunk length) but again, in any one population this is quite variable and usually correlated to the size of the animal. The trunk seems to grow faster than this organ so that, as a percentage of trunk length, the nephridium becomes “smaller” as the animal gets bigger. In *P. strombus* the nephridium length ranges from 50–20% in 4–27 mm worms while in *P. tuberculosum* worms 3–36 mm long, these values range from 35–18%. In both groups there is a general trend but with much deviation, especially in the mid-size range, similar to *Phascolosma* species (Cutler, Cutler, and Nishikawa 1984). 3) Degree of attachment of the nephridium to the body wall has had significance for earlier systematists. The attachment in this genus consists of a series of very fine, fragile thread-like mesenteries extending between the nephridium and the adjacent body wall. The ontogeny of these strands is unclear but they are present in all of the recently collected and previously undissected specimens we have examined and, in general, the whole nephridium is anchored.

Occasionally, the distal 10–20% may appear “unattached” but in an organ commonly 2–6 mm long, this is insignificant especially since these strands can be broken even by the force of a stream of alcohol directed on the organ to clear away gametes.

In summary, except in a very general way or in unusual cases, these three character-states are of no value in differentiating species of *Phascolion*.

9. *Rectal caecum*. — This small appendix is usually found at the intestine/rectum junction but may be further anterior along the rectum. Its presence/absence is usually reported and presumed to be taxonomically significant. While this may be truly absent in some individuals, it is also possible easily to overlook it. It is also likely that during the dissection of these small worms, especially the coiled ones from gastropod shells, that the fragile gut can be torn, potentially destroying the caecum.

In Stephen and Edmonds (1972) the rectal caecum is asserted to be absent in seven species. Upon reading the original descriptions one finds that in five cases no mention was made about its presence or absence. In the other two, the statement was to the effect that a caecum was not seen and it was probably absent. In both of these latter cases the sample size was one specimen (*P. heteropapillosum* and *P. sumatrense*). It is probable that most members of this phylum have a rectal caecum and its apparent absence in an occasional worm has no taxonomic meaning.

Subgenera

Gibbs (1985) has proposed three subgenera based on the nature of the retractor muscles and the relationship of the esophagus to them. We accept his construct but modify it in two ways. The presence of numerous well-defined contractile vessel villi and numerous tentacles in *P. cirratum* justifies the erection of a separate taxon for this species. The subgenus *Phascolion* s.s. we here subdivide into two sets: one with retractor muscles of equal size, the second with dorsal retractor significantly larger than the ventral.

Subgenus *Phascolion* s.s. Théel, 1875

Diagnosis. — Retractor column divided for most of its length. Esophagus detaching from retractor column at point posterior to first separation of retractor muscles. Diameter of dorsal retractor muscle at least twice that of ventral muscle.

Type-species. — *Sipunculus strombus* Montagu, 1804.

Species included. — *P. abnorme*, *P. bogorovi*, *P. caupo*, *P. hibridus*, *P. medusae*, *P. megaethi*, *P. pharetratum*, *P. robertsoni*, *P. strombus*, *P. ushakovi*.

Subgenus *Isomya*, new subgenus

Diagnosis. — As for subgenus *Phascolion* s.s. except that diameters of dorsal and ventral retractor muscles equal or nearly so.

Type-species. — *Phascolion tuberculosum* Théel, 1875.

Species included. — *P. convestitum*, *P. hedraeum*, *P. lucifugax*, *P. microspheroidis*, *P. tuberculosum*.

Subgenus *Montuga* Gibbs, 1985

Diagnosis.—Retractor column divided only at posterior end. Esophagus detaching from retractor column at point anterior to first separation of retractor muscles.

Type-species.—*Phascolion lutense* Selenka, 1885.

Species included.—*P. lutense*, *P. pacificum*.

Subgenus *Lesenka* Gibbs, 1985

Diagnosis.—Retractor muscles completely fused over whole length to give entire retractor column.

Type-species.—*Phascolion cryptum* Hendrix, 1975.

Species included.—*P. collare*, *P. cryptum*, *P. hupferi*, *P. rectum*, *P. valdiviae*.

Subgenus *Villiophora*, new subgenus

Diagnosis.—As for subgenus *Lesenka* but contractile vessel with numerous distinct, true villi.

Type-species.—*P. cirratum* Murina, 1968.

Species included.—*P. cirratum*.

Remarks.—The villi, as a morphological character-state, are heavily weighted in other families. By using it at this subgeneric level (not generic) we are being conservative.

Key to *Phascolion* Species

- 1. Separate dorsal and ventral retractor muscles; esophagus continues along one of these posterior to subdivision 2
- Retractor muscles fused for most or all of length; esophagus separating from retractor prior to any subdivision 16
- 2. Dorsal and ventral retractor muscles of equal size; holdfast papillae weakly chitinized, if at all Subgenus *Isomya* ... 3
- Ventral retractor muscle much thinner than dorsal ($1/10$ – $1/2$); many with distinct chitinized borders on holdfast papillae Subgenus *Phascolion* s.s. ... 6
- 3. Holdfast papillae large but with no chitinized borders 4
- Holdfast papillae with weak border of chitin 5
- 4. Hooks 70–220 μ m, broad, recurved; 10–30 tentacles *P. tuberculosum*
- Hooks 60–70 μ m, blunt, strongly curved; more than 35 tentacles *P. lucifugax*
- Hooks 25–50 μ m, slightly recurved and sharp point; tentacles absent or reduced *P. microspheroidis*
- 5. Bluntly pointed, spine-like hooks, 30–90 μ m *P. hedraeum*
- Hooks broad based and recurved *P. convestitum*
- 6. Slender, digitiform tentacles, usually more than 35 7
- Broadly based, tapering tentacles, usually less than 35 8
- 7. U-shaped, chitinized holdfast papillae *P. robertsoni*
- Bulbous holdfast papillae with no chitinized borders *P. medusae*

8. Chitinized holdfast papillae absent 9
 – Chitinized holdfast papillae present 11
9. Tall, spine-like, Type I hooks *P. ushakovi*
 – Broad based, Type II hooks 10
10. Anterior of trunk with large, compact papillae, usually chitinized; no helical coil in gut, loops only *P. hibridus*
 – Anterior of trunk without chitinized papillae; helical coil of gut present *P. pharetratum*
11. Chitinized border of holdfast composed of discontinuous, granular units *P. bogorovi*
 – Chitinized border of holdfast forming continuous, smooth margin 12
12. Hooks claw-like, pointed (Type I) 13
 – Hooks curved, bluntly rounded (Type III) 14
13. Ventral retractor less than $\frac{1}{2}$ dorsal, usually at different anterior/posterior levels; anterior papillae with single tips *P. strombus strombus*
 – Ventral retractor $\frac{1}{2}$ – $\frac{3}{4}$ width of dorsal, at same level; anterior trunk papillae with 1–4 tips *P. strombus cronullae*
14. Holdfast papillae few and entirely covered by cone of chitin *P. caupo*
 – Holdfast papillae with thin border of chitin; no cone 15
15. U-shaped holdfast papillae; ventral retractor origin anterior to dorsal ...
 *P. abnorme*
 – V-shaped holdfast papillae on posterior tip of trunk; ventral retractor origin posterior to dorsal *P. megaethi*
16. Fusion of retractor muscles incomplete with 3, rarely 4, separate origins apparent Subgenus *Montuga* ... 17
 – Retractors fused into single column but cleft in origin sometimes apparent 18
17. Chitinized holdfast papillae present *P. pacificum*
 – Chitinized holdfast papillae absent *P. lutense*
18. Contractile vessel villi present; more than 40 tentacles
 Subgenus *Villiophora* *P. cirratum*
 – Contractile vessel villi absent; less than 30 tentacles
 Subgenus *Lesenka* ... 19
19. Chitinized holdfast papillae present 20
 – Chitinized holdfast papillae absent 22
20. Four primary tentacles plus many accessory ones *P. cryptum*
 – More than 15 normal tentacles; no accessory tentacles 21
21. Holdfast papillae with pale, chitin borders of U- or V-shape .. *P. valdiviae*
 – Holdfast papillae with 1–4 tall strongly chitinized and collapsed teeth/
 points *P. collare*
22. Anus on anterior end of trunk *P. rectum*
 – Anus on distal half of introvert *P. hupferi*

Systematic Section of *Phascolion*

Phascolion abnorme Fischer, 1895

Phascolion abnorme Fischer, 1895:15–16, fig. 12.—Stephen and Edmonds, 1972: 169–170.

Phascolion heteropapillosum Wesenberg-Lund, 1963:135–138, figs. 11–12.—Stephen and Cutler, 1969:116–117.—Murina, 1970:67; 1971a:82.—Stephen and Edmonds, 1972:177–178. (Not Cutler, 1977b:153.)

Material examined.—*P. abnorme*: ZMUH—Fischer's holotype and only specimen #2124. *P. heteropapillosum*: ZMUH—type cannot be found; ZIAS—Murina's stations 652 and 665 from Red Sea and Gulf of Aden.

This uncommon species has two retractors of unequal size, chitinized holdfast papillae, 10–30 tentacles, hooks which are rounded and recurved (Type III) and the intestine with both loops and a spiral. It is not well founded. The name *P. abnorme* speaks well to the condition of Fischer's worm. It is clear that prior to his examination of the specimen both its retractor muscles underwent severe damage, the dorsal subdividing into three longitudinal components along its mid-section. He mistakenly asserted that the anus was posterior to the nephridiopore. The anus is actually placed in the normal location about 4 mm anterior to the nephridiopore.

It is clear that Wesenberg-Lund (1963) misinterpreted the dorsal and ventral retractors in *P. heteropapillosum*. Analysis of her fig. 12 (1963) now makes it clear that it has the normal *P. strombus* configuration of a large dorsal retractor and a small ventral with two origins. Also the apparent loss of the type (and only specimen) weakens its foundation. This uncertainty led Cutler (1977b) to misidentify some Australian specimens (see *P. hedraeum*). The two records of Murina (1970, 1971a) from the Gulf of Aden and Red Sea are questionable. She does say that hers do not have an "underdeveloped" dorsal retractor but makes no mention of the ventral muscle. Our inspection of these worms showed them to be small and in poor condition, and the ventral retractor could not be seen. However, with reservations we are leaving the record in this species.

It is clear that *P. heteropapillosum* is conspecific with *P. abnorme* and is the more commonly used name. However, it now becomes the junior synonym despite the poor description and condition of *P. abnorme*.

Known distribution.—Off South Africa and in the Red Sea and Gulf of Aden, at depths of 30–180 m.

Phascolion bogorovi Murina, 1973

Phascolion bogorovi Murina, 1973:66–68, fig. 1.

Material examined.—ZIAS—Murina's holotype.

While there is only a single specimen of this deep-water taxon, it is well preserved, 28 mm long, and from a region not well sampled. The hooks are large (height 200–250 μm), slender and black (Fig. 5E). The holdfast papillae have granular chitinized deposits which sometimes separate, appearing as 'teeth' (1–4) on the posterior papillae. The anterior end of the trunk is black with large, clear, lemon-shaped papillae. The dorsal retractor is 2–3 times wider than the ventral and the gut has both loops and coils. With reservations, we propose no change in the status of this species; however, its morphology matches *P. strombus* except for the large, slender hooks and granular holdfast papillae. Additional collections in the area may show it to only merit subspecific rank.

Known distribution.—Peru-Chile Trench at 3960 m.

Phascolion caupo Hendrix, 1975

Phascolion caupo Hendrix, 1975:133–135, pl. 1, fig. B, pl. 4.

Material examined.—USNM—two paratypes, #39002; several previously unreported specimens from 100 m off Cape Lookout, North Carolina.

When Hendrix described this species he unfortunately overlooked the ventral retractor muscle. This is not hard to do if one opens the worm from the dorsal side as the large dorsal muscle (5–7 times broader than the ventral in most 8–16 mm worms) covers the small ventral one. If one looks under the dorsal, the thin ventral muscle can be seen with the attached esophagus and its two short origins just posterior to the end of the ventral nerve cord. In other ways the internal anatomy matches that of *P. strombus*.

Externally, the introvert is about the same length as the trunk and bears Type III hooks (20–35 μm tall). The holdfast papillae are dark, few (as low as 12 in a narrow band) and tall, and when flattened, appear to have an elongate shape (Fig. 1E, F). Hendrix (1975) asserted that these are not associated with epidermal papillae. Our observations suggest that the papillae have been completely covered by the secreted chitin. Some are transparent on these small worms. This differs from the common *P. strombus* in zoogeography and hook and holdfast morphology.

Known distribution.—SE United States, intertidal to shelf depths.

Phascolion cirratum Murina, 1968

Phascolion cirratus Murina, 1968a:1724, fig. 1; 1971a:82.

Material examined.—ZIAS—Murina's types; 36 newly collected specimens from the Arabian Gulf.

This species was based on four well-preserved, intact specimens which are well-described in Murina (1968a). The tentacles are very numerous and although not completely extended, appear to be dendritically branched—very unusual for this genus. It also possesses numerous digitiform contractile vessel villi. These two character-states are correlated and probably an adaptation to low oxygen tension in the shallow warm waters of the Red Sea.

On one individual with a 12 mm trunk (measured from nephridium), the introvert is 17 mm long and the anus is 2 mm from the tentacular crown (90% of distance). Although somewhat rugose it lacks chitinized holdfast papillae, has a single fused retractor muscle and scarce, small papillae on the introvert bulb. We saw no 100 μm hooks as Murina described.

In 1981 Saudi Arabian Tetra Tech, Ltd. conducted a study of the intertidal and subtidal benthos of the Arabian Gulf. We have identified 36 specimens of this species from sand, 6 ft depth in Monifa Bay and off Bandar al Mishab at 8 ft in grass beds. Unfortunately, they are poorly preserved, slightly dried out and all from gastropod shells. We found no true chitinized hooks, only scattered papillae. These all have many tentacles, a single fused retractor muscle and numerous contractile vessel villi. As in the type also, the anus is located very near the mouth (2–5 mm), well anterior to the nephridium.

Known distribution.—Red Sea and Arabian Gulf, from 1–70 m.

Phascolion collare Selenka, de Man, and Bülow, 1883

Phascolion collare Selenka et al., 1883:45–46, pl. 6, figs. 71–74.—Fischer, 1922a: 12.—Stephen and Edmonds, 1972:173–174.—Cutler, 1977a:144–145.—Cutler and Cutler, 1979a:105.—Edmonds, 1980:29–30, fig. 52.

Phascolion tridens Selenka et al., 1883:46–47, pl. 6, figs. 75–79.—Stephen and Edmonds, 1972:189.—Cutler, 1977b:153–154.

Material examined.—MNHU—syntype of *P. collare*, #967; specimens from 1961–62 *Calypso* cruise to South America and recently collected unreported specimens from 100 m off Cape Lookout, North Carolina. The type of *P. tridens* appears to be lost.

This species has a fused retractor column, blunt hooks, and well-defined holdfast papillae with chitinized borders. The alleged difference between this and *P. tridens* is the presence of holdfasts with three points in the latter. The form the chitin takes is sometimes unusual (similar to *P. caupo*) resulting in a tall cone, which has a long pointed apex. It is clear that in this population holdfast papillae usually have a single point but may produce 2, 3, or 4 points on a single individual papilla (Fig. 1G; see also Cutler 1977b; Cutler and Cutler 1979a). Therefore, the use of this single character-state to separate two species is erroneous. The hooks (Fig. 6F) are much like Selenka drew but on the syntype they seem more worn down and blunter. Internally the intestine consists of loose loops only, not a spiral.

The only specimen of Selenka's in Berlin was still in its gastropod shell, the introvert is withdrawn and it is about 22 mm long. The skin is thin and the internal organs are not well preserved. It is clearly not what Selenka looked at but is part of that original collection, so we have designated it a syntype.

Known distribution.—Malaysian Archipelago, Western Australia, East Africa, Brazil, and North Carolina, from 5–2000 m.

Phascolion convestitum Sluiter, 1902

Phascolion convestitus Sluiter, 1902:32–33, text-fig. 1, pl. 3, figs. 6–9.—Murina, 1971a:82.

Phascolion convestitum Stephen and Edmonds, 1972:175–176.

Phascolion mediterraneum Fischer, 1922b:20–22, text-figs. 13–20.—Stephen and Edmonds, 1972:181–182.—Saiz Salinas, 1980:61–63.—Gibbs, 1985:318.

Phascolion beklemischevi Murina, 1964a:65–68, figs. 14–15.—Stephen and Edmonds, 1972:172.

Material examined.—ZMUA—Sluiter's type-material, V.Si 48-2, 48-3. ZIAS—3 specimens identified by Murina from Gulf of Aden plus the holotype of *P. beklemischevi*. NHRS—#65 and 95, Fischer's types of *P. mediterraneum* plus two co-types from ZMUH.

This species has two retractor muscles of approximately equal size with the dorsal slightly larger in a few individuals. The dorsal retractor muscle has a single origin (may be artificially subdivided) and the ventral has two which usually straddle the ventral nerve cord just anterior to its termination. The esophagus on at least two worms is connected to the dorsal not the ventral retractor muscle. The holdfast papillae are variable, large and bulbous, down to small and compact

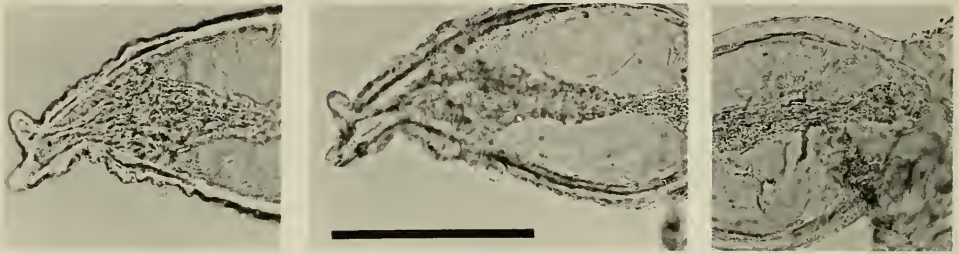


Fig. 8. Epizoa from anterior end of trunk of *P. convestitum*; different focal planes and at right, basal attachment to host. (Scale line = 0.1 mm.)

and only very weakly chitinized. Some have granular material around the border in disjunct units while others are without chitin and still others seem to have a slightly darker, smooth edge. There are about 20–25 normal tentacles and broad-based, recurved, pointed hooks, 50–100 μm tall (Fig. 6D). The gut is in loops with a few loose coils. There is a short, strong fixing muscle at the posterior end of the coil attached to the body wall between the roots of the ventral retractor which gives the misleading appearance of a spindle muscle.

Phascolion beklemishevi was described on the basis of one 4 mm specimen from the eastern Mediterranean. Our analysis of the holotype suggests that the presumed differences are not significant. This is a juvenile specimen in which the distal tip of the introvert has been damaged or torn; therefore, the alleged absence of tentacles is misleading. Hooks, however, are present and match those of *P. convestitum*. The two specimens from Mozambique (Cutler and Cutler 1979b) were re-examined and determined to be small *P. tuberculosum*, not *P. beklemishevi*.

Phascolion mediterraneum was described in 1922 on the basis of six specimens. In all of its major characters (hooks, retractors, holdfasts) it is like *P. convestitum*. The single alleged difference is in the form of the papillae on the anterior end of the trunk. Most of these are uni-tipped, mammiform or lemon-shaped glandular structures. However, in the *P. convestitum* population some have two or four “arms” or lobes projecting from the tip (Fig. 8). On one of Murina’s specimens there are present on the posterior end of the trunk. It is our judgement that these are probably not papillae but rather small epizoans, common in this genus.

This species is similar in many ways to *P. tuberculosum* and may only deserve subspecific rank but at this time we shall not propose any more change. The name *P. convestitum* now includes the two junior synonyms, *P. beklemishevi* and *P. mediterraneum*.

Known distribution.—Mediterranean, Red Sea, Gulf of Aden, and Indonesia, from 25–275 m.

Phascolion cryptum Hendrix, 1975

Phascolion cryptus Hendrix, 1975:127–133, pl. 1, fig. a, pls. 2–3.

Material examined.—USNM—10 paratypes, #39004; a few unreported specimens from 100 m off Cape Lookout, North Carolina.

This species with auxiliary tentacles where hooks are normally found, only four

primary tentacles, pale V-shaped chitin on holdfast papillae, and a fused retractor column is unique and well founded. When the introvert is drawn in, this form is externally very similar to *P. strombus* so one must examine the tip of the introvert and/or the retractor column. Ecologically it is distinct from *P. strombus* but is sympatric with *P. caupo*.

Known distribution.—SE United States, from 1–100 m.

Phascolion hedraeum Selenka, de Man and Bülow, 1883

Phascolion hedraeum Selenka et al., 1883:49–50, pl. 6, figs. 87–92.—Stephen and Edmonds, 1972:177.—Cutler and Cutler, 1979a:105; 1980c:2.

Phascolion dentalicola Sato, 1937:165–167, pl. 4, figs. 20–21, text-figs. 10–14.

Phascolion dentalicolum Stephen and Edmonds, 1972:172.—Murina, 1978:124.—Cutler, 1977a:145.—Cutler and Cutler, 1980b:194; 1981:72.—Cutler, Cutler and Nishikawa, 1984:274.

Phascolion kurchatovi Murina, 1974a:233–234, fig. 4.—Cutler and Cutler, 1980b:194.

Phascolion heteropapillosum.—sensu Cutler, 1977b:153.

Phascolion tuberculosum.—sensu Cutler and Cutler, 1980b:196.

Material examined.—BMNH—Selenka's types, plus 2 co-types in MNHU, #969; ZMUH—Fischer's specimen #V2120; 5 specimens of *P. dentalicolum* from locations in Northern Japan near type-locality (see Cutler and Cutler 1981); ZIAS—Murina's type of *P. kurchatovi* plus one specimen from South Atlantic (see Cutler and Cutler 1980b).

This now seems to be a distinct species based on a moderate number of individuals. It is generally less than 20 mm long and inhabits gastropod and scaphopod shells. The co-types at both museums were still in scaphopod shells but in good condition. Many of the shells still had scaphopods, not *Phascolion* in them.

The holdfast papillae are round with chitin around the anterior margin of the larger ones (80–300 μm) usually as a thin, pale border (Fig. 2C, D). A few from the Antarctic have a darker border. This denser material occasionally extends around the whole margin of the papillae. The bluntly pointed, slightly bent, spine-like hooks are 30–90 μm tall (Type I, very similar to that pictured for *P. strombus*; see also Fig. 2, Cutler and Cutler 1981). There are usually 20–30 tentacles. The two retractor muscles are of equal size and originate at the same level, posterior to the end of the ventral nerve cord at the end of the trunk. The dorsal has one, the ventral may have one but usually two origins. The esophagus follows the ventral retractor and the gut has one or two loops plus the spiral.

When Sato (1937) described *P. dentalicolum* he compared it to *P. mediterraneum* but made no reference to *P. hedraeum* or Fischer's record of it from Japan in his original or later more general papers.

When Cutler and Cutler were working with Brazilian collections they used a Brazilian name (Cutler and Cutler 1980c) but when in Japan they fell into a familiar trap of using a Japanese name without doing enough comparison with *P. hedraeum*.

Murina's (1974a) differential diagnosis of *P. kurchatovi* emphasized the well-developed holdfasts and retractors with one root each. While our analysis of the holotype confirms these observations, they are within the total range of variation

for the population. All other characters match those of *P. hedraeum*. The only other use of the name *P. kurchatovi* is in Cutler and Cutler (1980b) describing a specimen without hooks. However, it should also be considered *P. hedraeum*.

An uncritical interpretation of Wesenberg-Lund's (1963) description of *P. heteropapillosum* caused Cutler (1977b) to misidentify some Australian specimens which are here determined to be *P. hedraeum*. A re-examination of Cutler and Cutler's (1980b) "Vema" material in this genus showed a misapplication of the name *P. tuberculosum* to one specimen which is hereby corrected.

From a reevaluation of the literature and an analysis of the above material, we conclude that the three species, *P. hedraeum*, *P. dentalicolum* and *P. kurchatovi* are conspecific and thus *P. hedraeum* becomes the senior synonym.

Known distribution.—Several southern hemisphere records from 65°S up to South Africa, Uruguay, and Brazil in the Atlantic; in the S. Pacific including the Great Australian Bight and Tasman Sea, and also off Japan, generally at shelf and slope depths ranging from 7–4610 m.

Phascolion hybridus Murina, 1981

Phascolion hybridus Murina, 1981:348–349, 6 figs.

Material examined.—ZIAS—Murina's holotype and paratypes.

This species is characterized by having retractor muscles of unequal size (the origin of the larger dorsal is incompletely fused). The Type II hooks are broad-based (like *P. tuberculosum*) but pale and about 40 μ m tall. The midtrunk is smooth, lacking any holdfast papillae. On the anterior end of the trunk are large, mammiform, single-tipped papillae which appear to be chitinized. These do not, however, form a compact unit which would appropriately be called a shield, although Murina used this term. We consider this a unique and valid species.

Known distribution.—Malaysia and Samoa, at 1530–2380 m.

Phascolion hupferi Fischer, 1895

Phascolion hupferi Fischer, 1895:16–17, figs. 16–18; 1914:77.—Stephen and Edmonds, 1972:179.

Phascolion indicus Murina, 1974b:282–283, fig. 1.—Cutler, Cutler, and Nishikawa, 1984:275–276.

Material examined.—ZMUH—Fischer's syntypes, #V2036, V2037; recently collected material from Japan and the Ivory Coast; ZIAS—Murina's holotype of *P. indicus*.

With one major exception Fischer's description is accurate. We examined several of his worms which had not been removed from their mollusc shells and the nature of the papillae is more variable than he described. The anus is located about 50–75% of the way towards the mouth and, while difficult to count accurately due to retracted introverts, there are more than 12 tentacles. It seems unlikely that these would have 40 tentacles as Fischer reported. The fusion of the retractor muscles into a single column seems to be complete in most, but in a few worms it exhibits two origins (a small cleft) or is torn or shredded towards the posterior. This muscle does originate from the posterior end of the trunk, not the middle as was originally stated (the major flaw in Fischer's description).

When Murina (1974b) described *P. indicus* she differentiated it from *P. hupferi* on the basis of its retractor origin (posterior vs middle of trunk) and longer papillae at the end of the trunk. Cutler, Cutler, and Nishikawa (1984) concluded that the two entities were distinct but it is now clear, as a result of this study, that they were mistaken and that these two are conspecific. The differences really are superficial, external and not significant or consistent.

Known distribution.—Japan, S. of Java, and W. Africa, from 10–1010 m.

Phascolion hedraeum Selenka, de Man, and Bülow, 1883

Phascolion lucifugax Selenka et al., 1883:43–44, pl. 5, figs. 64–66.—Stephen and Edmonds, 1972:180.

Material examined.—MNHU—Selenka's syntype #966.

This species is represented by three animals. The one from Hokkaido, Japan, is now completely dried. The two from Bohol, Philippines, were still in their gastropod shells and therefore not really examined by Selenka; one of these, when removed from the shell was still in good condition. It is about 40 mm long with the introvert entirely withdrawn. The intestine is in loops only, exhibiting no coils. The two retractor muscles are each about 1.5 mm broad and the esophagus, which carries a large vesicular contractile vessel is attached to the ventral muscle. Both retractors have their origins about 6 mm from the posterior end of the trunk, the ventral origin is slightly divided and posterior to the dorsal.

Externally the medium-sized (65–70 μm), blunt hooks (Fig. 6G) are of Type III. The holdfast papillae have not produced chitin (*tuberculosum* type) and there are more than 30 long, slender tentacles. This combination of characters is closest to *P. tuberculosum* but different enough (tentacle number, hook shape, retractor origins) so that, with some reservations due to the small sample size, we propose no change in the rank of this taxon.

Known distribution.—Philippines and N. Japan, at unknown but probably shelf depths.

Phascolion lutense Selenka, 1885

Phascolion lutense Selenka, 1885:16–17, pl. 4, figs. 22–23.—Fischer, 1928:484.—Murina, 1957:1781–1790, figs. 4a–b, 5a–d; 1961:140–142, fig. 1; 1971b:43; 1972:305–306; 1974a:235; 1978:124.—Stephen and Edmonds, 1972:180–181.—Cutler, 1977b: 145–146.

Phascolion canum Cutler and Cutler, 1980a:454–456, fig. 2.—Gibbs, 1985:321.

Phascolion species.—Cutler and Cutler, 1980b:197.

Material examined.—BMNH—Selenka's type; 8 of Murina's specimens from the Pacific Ocean; USNM—type of *P. canum* plus newly collected Northeast Atlantic specimens.

The original description was based on three individuals but subsequent collections of many worms (by Murina among others) have established a firm foundation for this species. As in other populations, some individuals lack hooks (Selenka's 15–20 mm worms) but most have pale, Type I hooks, 40–150 μm . This species has the retractor muscles fused for much of their length, leaving three, sometimes four distinct origins, and the esophagus leaves the retractor column on the fused

portion. Externally the smooth body surface (with small, densely-packed papillae at the anterior end and inconspicuous skin bodies in the mid trunk of some but no holdfast papillae) is characteristic. This may be associated with their life in clay/mud tubes and not mollusc shells.

Selenka (1885:17) said that "The tentacles are short and small . . . are few in number, at most 16." His three specimens had completely retracted introverts. In some recently collected material from the Northeast Atlantic Ocean we found one worm with an extended introvert showing what appears to be a continuous folded membrane surrounding the mouth but it may be several lobes like in *P. pacificum* (Fig. 7B).

When *P. canum* was originally described the retractor muscles were interpreted as "two in number united for about half their length, the dorsal with two long branches and the ventral with two short ones." It was compared to species with two retractor muscles and not to *P. lutense* which was said to have one muscle with three roots. This difference is a matter of semantics, as well as the variability that is present in this population, and partially a reflection of the state of contraction of the introvert. It is now clear as the result of this analysis that these two forms are the same. The holotype of *P. lutense* is larger and a little rougher-skinned than other specimens and lacks the grey mud cap, probably due to being in alcohol since 1885.

Known distribution.—This deep water species (1820–6860 m) is found in the southern hemisphere (36–66°S) in the Pacific Ocean, off Argentina, and in the SE Indian Ocean. It has also been found in the NW Pacific and the Bay of Biscay but is apparently absent in the lower latitudes.

Phascolion medusae Cutler and Cutler, 1980

Phascolion medusae Cutler and Cutler, 1980c:2–4, figs. 1–3.

Material examined.—AMNH—type-specimens #4023.

We have nothing to add to the recent description of this species except to figure the hook (Fig. 6E). It has a dorsal retractor several times larger than the ventral, introvert hooks, many slender tentacles, and large holdfast papillae without chitinous borders. The comment about the esophagus paralleling the dorsal retractor (Cutler and Cutler 1980c:3) could be misleading. It is attached to and masks most of the ventral muscle which does parallel the dorsal. There are a number of similarities between this and *P. robertsoni*.

Known distribution.—S. Brazil, from 166–338 m.

Phascolion megaethi Cutler and Cutler, 1979

Phascolion megaethi Cutler and Cutler, 1979b:961–964, figs. 10–12.

Material examined.—MNHN—type material #AH-413.

There is nothing new to add to the recent description of this species except the small (30–35 μ m), blunt hooks are of Type III like those in Fig. 6F. Its separation from other members of the *P. strombus* group is based on the fused ventral retractor originating posterior to the dorsal, the large red anterior trunk papillae, smooth trunk except for a few, small, chitinized, V holdfasts at the posterior tip and its hooks.

Known distribution.—S. Madagascar, intertidal.

Phascolion microspheroidis Cutler and Duffy, 1972

Phascolion microspheroidi Cutler and Duffy, 1972:71–76, figs. 1–3. Not *Phascolion microspheroides* Cutler and Cutler, 1980a:456.

Material examined.—USNM—type-material; recently collected North Atlantic specimens.

This small species (trunk usually less than 5 mm) with two retractors of equal size, no chitinized holdfast papillae and small pointed hooks (Fig. 5C, D) remains distinct. The ventral retractor pair may remain unfused for about one-fourth its length (longer than in most species).

So far this is not known to occur outside the western North Atlantic. Those from the Bay of Biscay and Mediterranean reported in Cutler and Cutler (1980a) have been reexamined and in light of our present understanding have been transferred to *P. tuberculosum*. Small *P. tuberculosum* (less than 3 mm) strongly resemble *P. microspheroidis* in many ways but the former has larger anterior papillae and the hooks are distinctive.

Known distribution.—East Coast of United States from 31–40°N, at 490–1700 m.

Phascolion pacificum Murina, 1957

Phascolion pacificum Murina, 1957:1777–1781, text-figs. 2a–b, 3a–e; 1971b:43; 1972:306; 1973:70; 1974a:235; 1978:125.—Stephen and Edmonds, 1972:184.—Cutler, 1977a:146.—Cutler and Cutler, 1980b:194.—Cutler, Cutler, and Nishikawa, 1984:276–277.—Gibbs, 1985:319–321.

Material examined.—ZIAS—Murina's holotype plus other material collected and identified by her; recently collected material from Japan.

This species with retractor muscles fused for most of their length into a single column with two, three, or four separate origins, Type I hooks and holdfast papillae with a thin chitin border is well founded. The extent of fusion of the retractor muscles is quite variable but the esophagus always separates before any split. Externally it has many similarities to *P. strombus* with pale U or V shaped holdfasts of variable thicknesses which may have led to some misidentifications in the past. For instance, reexamination of some *P. strombus* from the Gulf of Gascone (Cutler and Cutler 1980a) showed some to be *P. pacificum*. The chitinous holdfasts appear thinner and paler than most *P. strombus*. Internally this is also very similar to *P. lutense* but the latter lacks chitinized holdfast papillae. Murina described this species as having 16 tentacles. All her specimens which we saw at ZIAS had retracted introverts, were small and not in prime condition. We saw nothing that looked like a normal array of tentacles. On our recently collected material from Japan and Gibbs' from the Bay of Biscay, the tentacles are found to be reduced to lobes.

Known distribution.—This bathyal and abyssal species (300–6860 m) is widespread at high latitudes in the northwest and southwest Pacific, the southeast and South Atlantic, and the sub-Antarctic Indian Oceans. The only records at lower latitudes are in the Peru-Chile Trench at depths from 5760–6860 m.

Phascolion pharetratum Sluiter, 1902

Phascolion pharetratum Sluiter, 1902:31–32, pl. 3, figs. 3–5.—Stephen and Edmonds, 1972:186.—Cutler and Cutler, 1979b:964.

Material examined.—ZMUA—Type-material, V.Si. 48-4, 48-5.

The absence of chitinized holdfast papillae, introvert retractor muscles of unequal size originating from some distance anterior to the back end of the trunk, and the hook shape (Fig. 6C) seem to set this taxon apart. In many ways the written description resembles *P. medusae*.

Between 1982, when we made a preliminary examination of the damaged specimens in Amsterdam, and 1984, the material had been misplaced and unavailable for closer examination. However, despite this problem we propose no change in the status of this species. Our Madagascar specimens fit Sluiter's description fairly well except that the hooks are somewhat more bent as in *P. lucifugax*.

Known distribution.—Indonesia and S. Madagascar, from 1–91 m.

Phascolion rectum Ikeda, 1904

Phascolion rectus Ikeda, 1904:15–18, text-figs. 45–49.—Sato, 1939:413.

Phascolion rectum Stephen and Edmonds, 1972:186–187.—Cutler and Cutler, 1981:74.—Cutler, Cutler, and Nishikawa, 1984:277–278.

Material examined.—Eleven specimens from Honshu, Japan; the type cannot be located.

There is nothing new to add to our earlier comments on this species. It has the fused retractor muscles and lacks both hooks and chitinized holdfast papillae. The gut has a spiral and there are fewer than 12 tentacles. Except for the anus location on the anterior trunk it is very similar to the sympatric *Phascolion hupferi*.

Known distribution.—Central Japan, at 30–2600 m.

Phascolion robertsoni Stephen and Robertson, 1952

Phascolion robertsoni Stephen and Robertson, 1952:439–441.—Stephen and Cutler, 1969:117.—Stephen and Edmonds, 1972:187.

Material examined.—RSM—two paratypes #1958.23.76–79.

This uncommon species is distinct and well founded, despite an error in the original description of the retractor muscles. There are two, not one, retractor muscles, of unequal size. The dorsal is about three times larger than the ventral and originates a few millimeters anterior to the ventral which is at the posterior end of the trunk. The esophagus follows the ventral retractor and the gut has only loops, no spiral. The nephridiopore is posterior to the anus.

Externally there are about 40 slender tentacles (Fig. 7A) and many small (30–40 μm) blunt, Type III hooks. The holdfasts on the trunk are scattered, pale, 100–200 μm wide, U or V shaped and associated with large, bulbous papillae. Additionally, there are pale, chitinized papillae on the basal part of the introvert—a unique feature of unknown function.

Known distribution.—E. and S. Africa, from 1–60 m.

Phascolion strombus (Montagu, 1804)

Sipunculus strombus Montagu, 1804:74–76.

Phascolion strombi Stephen and Edmonds, 1972:187–189 (see this for records and synonymy before 1969).—Stephen and Cutler, 1969:117.—Murina, 1970:

- 67; 1978:123; 1971a:83; 1972:306.—Cutler, 1973:168–173; 1977a:146.—Zavodnik and Murina, 1975:127; 1976:84.—Gibbs, 1977:22–23.—Cutler and Cutler, 1980a:456; 1980b:194–195.—Ocharon, 1980:116–117.—Saiz Salinas, 1980:63–66.—Frank, 1983:21–22.—Cutler, Cutler, and Nishikawa, 1984:278–279.
- Phascolion strombi africanum* Cutler and Cutler, 1979b:964–965; 1980b:196.
- Phascolion africanum* Fischer, 1923:5.—Wesenberg-Lund, 1963:134–135.—Stephen and Cutler, 1969:117.—Stephen and Edmonds, 1972:170.
- Phascolion anomalus* Murina, 1981:349–352, 4 figs.
- Phascolion alberti* Sluiter, 1900:9–10, pl. 1, figs. 1–2, pl. 3, figs. 1–2; 1912:17–18.—Gerould, 1913:416.—Murina, 1964a:63–65, fig. 12.—Stephen and Edmonds, 1972:170–171.—Gibbs, 1985:317.
- Phascolion artificiosus* Ikeda, 1904:18–20, text-figs. 50–55.—Sato, 1939:413.
- Phascolion artificiosum*.—Stephen and Edmonds, 1972:171–172.—Cutler and Cutler, 1981:70–71.—Cutler, Cutler, and Nishikawa, 1984:273–274.
- Phascolion brotzkajae* Murina, 1964a:68–70, figs. 16–17.—Stephen and Edmonds, 1972:172.—Murina and Zavodnik, 1979:251–252.
- Phascolion tortum* Edmonds, 1976:218–222, figs. 7–11.—Murina, 1978:125.

Material examined.—ZIAS—Murina's holotypes of *P. anomalus* and *P. brotzkajae*; two reference specimens of *P. tortum* from the type-locality identified by S. Edmonds; many recently collected specimens from the Atlantic, Arctic, and Pacific Oceans.

This species has two retractor muscles of unequal size, the ventral being significantly smaller than the dorsal, holdfast papillae with chitinized borders (Fig. 1A–C), 10–30 well-developed tentacles, and sharp, claw-like hooks (Fig. 5A, B). It has the longest and most complex history with the most junior synonyms of any species in this genus. It is very widespread and common. Many authors have discussed its extreme plasticity of form, notably Théel (1875a, 1905, where he also presented excellent illustrations), Gerould (1913) and Fischer (1923). An analysis of 2700 specimens from the U.S. East Coast supported these earlier assertions of variability within a population (Cutler 1973).

As part of this present work we made more detailed measurements of internal and external characters to attempt a more objective approach. The material we had from several parts of the world's ocean (80°N to 60°S) was even now disconcerting because of the apparent, superficial differences. One can easily see why Théel (1875b) thought *P. spitzbergenense* was a separate form only to withdraw that viewpoint 30 years and many worms later. A particularly interesting problem was presented by our Japanese collections (Cutler, Cutler, and Nishikawa 1984). There are two morphs there, differing in holdfast shape, hook size, and origin of the ventral retractor. In all cases these character states fall within the range of the North Atlantic population but one towards one extreme, the second towards the other. Our present view is that these may represent the two terminal points in a "Rassenkries" assuming a center of origin in the North Atlantic and one population going eastward over the Siberian/Asian Arctic, the second dispersing westward over the Canadian Arctic to meet in the North Pacific. The data base is inadequate to test this hypothesis so it remains speculative for the present. The concept of a polytypic species would easily apply to *P. strombus*. Gene frequencies have clearly shifted as dispersal occurred over the globe but until breeding ex-

periments or at least some biochemical or cytogenetic work can be done, we have only our 20 years of experience with the group to aid us.

Junior synonyms of Phascolion strombus.—Gerould (1913) changed the status of *P. tubicola* to that of a subspecies but Stephen and Edmonds (1972), while leaving it as a subspecies (p. 188) also resurrected it to specific rank with no explanation (p. 190). In addition, Gerould named six varieties which Stephen and Edmonds elevated to subspecific rank with the comment, "We are not certain if they are all true subspecies . . ." Both Wesenberg-Lund (1929) and Cutler (1973) noted that these varieties have little systematic value, ". . . we do not have seven constant combinations of characters; the characters may be found in numerous different combinations even from any one locality" (Cutler 1973:170). We reaffirm that position and treat these names as junior synonyms.

Phascolion africanum: The essence of this taxon is elusive. The apparent geographic isolation, lack of pointed holdfasts and a larger number of tentacles led us to retain the name at the subspecies level (Cutler and Cutler 1979b, 1980b). Based on our current knowledge we conclude that these presumed differences are not significant and *P. africanum* is now considered a junior synonym of *P. strombus* without subspecific status.

Phascolion alberti: In Cutler's (1973:169) discussion of *P. strombus* he stated ". . . *P. alberti* is not a distinct biological entity, but merely a form of *P. strombi*." Gibbs (1985) formally synonymized this taxon under *P. strombus* and we concur.

Phascolion anomalus: This was described from the Bay of Biscay on the basis of a single 10 mm worm. The peculiar dorsal retractor muscle is the only character which would distinguish this from *P. strombus*. It is our conclusion that the partitioning of this large muscle into what Murina called 'supplemental muscles' is the result of some trauma or ontogenetic anomaly, not a natural condition.

Phascolion artificiosum: The 18 worms reported in the literature presumably differ from *P. strombus* in lacking hooks. As noted in the section on morphological characters this character state can be misleading. Ikeda (1904) unfortunately had also confused the dorsal and ventral retractor muscles and his fig. 55 is misleading; the esophagus comes off the ventral, not dorsal retractor so that it has the typical *P. strombus* morphology. We now believe this entity represents only a few hookless individuals in the large sympatric *P. strombus* population.

Phascolion brotzkajae: This single 4 mm worm with retracted introvert was differentiated from *P. strombus* on the basis of two presumed differences: the absence of tentacles and the split in the dorsal retractor. The original description was brief and the report of a second worm (Murina and Zavodnik 1979) added nothing to the description. If tentacles were present they would be extremely hard to see in such a small worm with its introvert not expanded. We were unable to verify presence or absence due to size and condition of the holotype. The dorsal retractor is as described but could be due to unfinished ontogeny. Whether real differences or artifacts, we believe these two worms are representatives of a *P. strombus* population.

Phascolion tortum: When Edmonds (1976) described *P. tortum* he used three characters to differentiate it from *P. strombus*: the ventral retractor was more slender, was shifted anteriorly (mid-third), and it had a large contractile vessel. We affirm the last condition but suggest that a similar situation exists in many *P. strombus* populations and is not diagnostic. The ventral retractor muscle in

the two worms we had (5 and 9 mm long) originated only 15% of the distance from the posterior end of the trunk, not the mid-third (33–67%). The dorsal is 4 and 5 times the size of the ventral. Both of these states are within the range of the Eastern Atlantic and Japanese populations, not necessarily in the same individuals.

Known distribution.—This is a very common and eurytopic North Atlantic and Arctic species also found in deep water in the Caribbean. There are scattered reports from the Mediterranean, Red Sea, Gulf of Aden, Madagascar, and South Africa. There are two Antarctic records plus off Argentina and Chile. Other Pacific Ocean records come from the South Pacific, New Zealand, and Japan. It is known from depths of 1–4030 m.

Phascolion strombus cronullae Edmonds, 1980, new status

Phascolion cronullae Edmonds, 1980:30–32, figs. 46–51.

Material examined.—Three reference specimens from the type-locality, identified by S. Edmonds.

When Edmonds erected this taxon he assigned it to the species category, weighting heavily the anterior trunk papillae which may have 2, 3, or 4 tips or points. While it is true that some (about 25%) of the anterior papillae have multiple tips, most have a single point like that found in *P. strombus*. Perhaps a more significant difference is the relationship between the size of the dorsal and ventral retractor muscles: the dorsal is 1.5–2 times the size of the ventral and originates at about the same level very near the posterior end of the trunk thus being the only known “bridge” between the “strombus” and “tuberculosum” morph as discussed earlier. Its hooks, holdfast papillae, and other characters still match well that of the nominate form. It is geographically isolated and the differences in retractor and papillae morphology are considered sufficient for subspecific rank.

Known distribution.—New South Wales, Australia.

Phascolion tuberculosum Théel, 1875

Phascolion tuberculosum Théel, 1875b:15–16, pl. 1, fig. 1, pl. 3, fig. 16.—Stephen and Edmonds, 1972:190.—Cutler and Cutler, 1980a:456–457.—not Cutler and Cutler, 1980b:196.—Gibbs, 1985:317–318.

Phascolion beklemishevi.—sensu Cutler and Cutler, 1979b:961.

Phascolion hirondellei Sluiter, 1900:7–9, pl. 2, figs. 1–6.—Stephen and Edmonds, 1972:178.—Gibbs, 1985:318.

Phascolion pallidum Koren and Danielssen, 1877:132–134, figs. 22–24.—Selenka et al., 1883:42–43.—Leroy, 1936:425.—Stephen and Edmonds, 1972:184.

Phascolion temporariae Edmonds, 1976:217–218, figs. 1–6.

Phascolion microspheroides.—sensu Cutler and Cutler, 1980a:456.

Material examined.—*P. tuberculosum*: NHMS—Théel’s type, #233; numerous recently collected specimens from the North Atlantic. *P. hirondellei*: MOMV—four of Sluiter’s syntypes (St. 66, 112, 184). *P. pallidum*: ZMUB—Koren and Danielssen’s type. *P. temporariae*: reference material from type-locality identified by S. Edmonds.

This is one of the better known species in this genus and is characterized by



Fig. 9. Papillae on anterior end of trunk of *P. tuberculosis* showing variable number of tips on a single worm. (Scale line = 200 μm .)

the large (70–220 μm), broad, recurved hooks (Fig. 6A, B show its massiveness and internal structure). The holdfast papillae are large (80–330 μm), spherical and without chitinous borders (Fig. 2A, B), but occasionally one sees some granular material gathered along the anterior margin. The two retractor muscles originate near the posterior end of the trunk at nearly the same level. The ventral may originate 1–6% (rarely up to 10%) of the trunk length anterior to the dorsal (this distance is commonly 0.5–2 mm) and could be easily overlooked). These are usually of equal width but may vary so that the ventral is from 0.75–1.25 times the dorsal muscle. The large mammiform papillae around the anterior end of the trunk usually have one protruding tip but some have two (others up to 4) tips (Fig. 9). The frequency of multiple-tipped papillae varies from specimen to specimen. Commensal epizoans are also common here.

The similarity of *P. hirondellei* to *P. tuberculosis* is obvious despite the poor condition of the syntypes. The description of *P. hirondellei* was misleading in that the retractors are of equal size (although traumatized); the hooks measure 100–200 μm of a typical *P. tuberculosis* morphology, and the “thread-like papillae” are in fact epizoid hydrozoans.

Phascolion temporariae was presumed to be distinct because of having only single-tipped anterior papillae; however, some *P. tuberculosis* also have only single-tipped papillae. It is also described as having holdfasts while *P. tuberculosis* has none. This is a matter of perception and semantics. A side-by-side comparison shows no significant differences—both have large holdfast papillae which may occasionally show aggregation of denser material along one border. This Australian population may deserve subspecific rank but we would have difficulty defining it.

Known distribution.—Common in the NE Atlantic including the Azores, Mid-Atlantic Ridge, Bay of Biscay, and Scandinavian waters at bathyal depths (25–2700 m). A few specimens from Japan and New Zealand from 93–300 m suggest

a presence in the Pacific also. The sole Caribbean record cannot be confirmed and is doubtful.

Phascolion ushakovi Murina, 1974

Phascolion ushakovi Murina, 1974b:284–285, figs. 1–3.

Material examined.—ZIAS—Murina's type material.

This species has several distinctive characters: 1) the many tall, black, spine-like hooks (Fig. 5F); Murina's fig. is misleading as it is not a side view; 2) the very thin ventral retractor muscle ($\frac{1}{5}$ to $\frac{1}{10}$ the size of the dorsal) and 3) the external papillae. On the anterior and posterior ends are large, dark, mammiform papillae (like *P. tuberculosum*) but in the mid-trunk there are no holdfast papillae, only flattened skin bodies. The gut coil is attached by several fixing muscles, the posterior one, coming from inside the gut coil and having a large diameter, was incorrectly called a spindle muscle.

Known distribution.—W. Australia at 330 m.

Phascolion valdiviae valdiviae Fischer, 1916

Phascolion valdiviae Fischer, 1916:16; 1922a:13, pl. 2, figs. 7a–g.—Stephen and Edmonds, 1972:191–193.—Cutler and Cutler, 1979b:965.

Material examined.—MNHU—Fischer's type, #6073.

This species has been reported from four disjunct locations in or near the Indian Ocean and was based on a total of five specimens prior to Cutler and Cutler (1979b). It has retractor muscles which are almost entirely or entirely fused into a single column and holdfast papillae with variably formed chitinized margins present. The pale, Type I hooks (70–90 μm) are usually but not always present. This subspecies has hooks and holdfast papillae with little chitin, mostly semi-circular in shape.

Known distribution.—St. Paul's Island and off Durban.

Remarks.—When Fischer first described *P. valdiviae* he created two subspecies, *P. valdiviae valdiviae* and *P. valdiviae sumatrense* but a few years later elevated each to specific rank (1922a). Twenty years later Stephen (1941) found one worm and with no reference to *P. valdiviae* or any other species named a new species, *P. murrayi*. Internally it cannot be differentiated from *P. valdiviae*. The nature of the holdfast papillae does appear to differ in the amount of chitin produced. Two of the taxa (four specimens with 15–25 mm trunks) lack introvert hooks. From their overall similarity and geographic proximity we conclude that they are conspecific and return to Fischer's original treatment of *P. valdiviae sumatrense* as a subspecies placing *P. murrayi* in synonymy with it.

Phascolion valdiviae sumatrense Fischer, 1916

Phascolion valdiviae var sumatrense Fischer, 1916:17.

Phascolion sumatrense Fischer, 1922a:13–14, pl. 2, fig. 7a.—Stephen and Edmonds, 1972:191.

Phascolion murrayi Stephen, 1941:407, pl. 2, fig. 5.—Stephen and Edmonds, 1972:183–184.

Material examined.—*P. v. sumatrense*: MNHU—Fischer's type, #6074; *P. murrayi*: BMHN—type.

This subspecies differs from the nominate form by having chitinized holdfast papillae more variable with U, V and circular shapes on the posterior half of the trunk (except the last 10%), seeming to lack hooks (in larger worms), and being known from a different part of the Indian Ocean.

Known distribution.—Sumatra and Gulf of Aden at 750–1295 m.

Species Placed in Incertae Sedis or Species Inquirendum

Phascolion botulus Selenka, 1885

Phascolion botulus Selenka, 1885:18, pl. 4, fig. 20.

Phascolion botulum Stephen and Edmonds, 1972:173.

Material examined.—BMNH—Selenka's holotype.

This species was described on the basis of a single, damaged, incomplete individual said to have two retractor muscles of unequal size, holdfasts, but lacking hooks (like *P. artificiosum* and *P. sandvichi*). The type-material in London consists of the partially dehydrated introvert and about 10% of the trunk. It is therefore impossible to answer several critical questions and this name must be placed on the list of *incertae sedis*.

Phascolion ikedai Sato, 1930

Phascolion ikedai Sato, 1930:20–23, pl. 3, figs. 13–17, text-figs. 6–9.—Stephen and Edmonds, 1972:179–180.—Cutler and Cutler, 1981:74.—Cutler, Cutler, and Nishikawa, 1984:274–275.

Material examined.—ZITU—4 specimens identified as this by Sato but still in shells.

When Cutler and Cutler (1981:74) discussed this species they concluded by making no change in its status but were not completely comfortable with it. After this examination of the genus, our discomfort has increased and we can no longer consider this a valid taxon. The type-material is lost and the four worms we found identified by Sato had never been removed from their coral-encased mollusc shells. Their poor state of preservation makes it impossible to answer the critical questions, i.e., because he did not figure or mention esophagus on retractor column, did Sato overlook a small ventral retractor muscle with esophagus attached? If he had, then it would be the same as *P. strombus* (see Cutler and Cutler 1981). What about nephridiopore/anus relationship? If the nephridiopore were actually anterior it would be the only one in this genus.

It now seems most prudent to transfer this untestable entity to the status of *species inquirendum* pending future clarification.

Phascolion manceps Selenka, de Man and Bülow, 1883

Phascolion manceps Selenka et al., 1883:44–45, pl. 1, fig. 2, pl. 5, figs. 67–70.—Shibley, 1899:154.—Stephen and Edmonds, 1972:181.

Material examined.—None.

Neither the type-material nor Shibley's specimens can be located. The original

description is not clear about the location of the anus or the length of introvert. Stephen and Edmonds' (1972) translation further confuses the description of the nephridium. Our interpretation of the original is that the anus is located posterior to the mouth (on the introvert); the introvert is short only if measured from the anus to tentacles; and the nephridium is in the trunk, far behind the anus, not extending from the posterior of the trunk to near the anus. The contractile vessel tubules are also peculiar, unlike other members of this genus (except *P. cirratum*). Théel (1905:12–13) clearly thought it should be an *Onchnesoma*. Being unable to verify any of these features, we place this taxon the list of *Incertae sedis*.

Phascolion moskalevi Murina, 1964

Phascolion moskalevi Murina, 1964b:255–256, figs. 2–3.—Stephen and Edmonds, 1972:183.

Material examined.—ZIAS—Murina's holotype.

Although this single specimen has only one nephridium and fused retractor muscles, other characters indicate that it does not belong in this genus. These are: hooks in rings, a spindle muscle present, although unattached posteriorly, and the complete absence of holdfast papillae. Also the retractor muscles are obviously two fused ventrals originating from mid-trunk, unlike *Phascolion*. Hendrix (1975) discussed this species and suggested it might be a *Golfingia*. Upon examination of the holotype we found that the description of the tentacles (only 5 on one side) is correct but due to damage, not the natural array. The fusion of retractors and presence of one nephridium suggests some teratogenetic or ontogenetic anomaly. We place this species on the list of *species inquirendum* until further material is found.

Phascolion parvum Sluiter, 1902

Phascolion parvum Sluiter, 1902:30–31, pl. 3, figs. 1–2.

Phascolion parvum Stephen and Edmonds, 1972:185.

Material examined.—ZMUA—V.Si. 48-3, 48-4, 48-6 containing shells and a total of four incomplete, fragile specimens.

Due to the incomplete and/or damaged nature of this material it is impossible to verify Sluiter's description. On one animal the retractor muscles are about equal sized but seem to originate from the posterior end of the trunk not the middle as Sluiter stated. Hooks are absent on one worm and present in a second vial on a free floating piece of tissue.

No subsequent collections of this species have been made. The foundation for this species is not sound so until and unless additional specimens are collected to provide a tangible basis, we place this name on the list of *species inquirendum*.

Phascolion sandvichi Murina, 1974

Phascolion sandvichi Murina, 1974b:283–284, fig. 2.

Material examined.—ZIAS—Murina's holotype.

This single 9 mm worm appears to have a peculiar suite of characters: the retractors are approximately of equal size (dorsal 1.25 times ventral) but the dorsal

appears to have 3 origins; hooks are absent; the holdfast papillae have granular borders, some appearing as discrete bumps; and the posterior fixing muscle is unusually well developed looking like a spindle muscle, but it begins (ends?) within the gut coil.

Because of this combination of characters which may not be natural, and the inadequate sample size, we place this species on the list of *species inquirendum* pending further study if more specimens become available.

Genus *Onchnesoma* Koren and Danielssen, 1875

Type-species. — *Onchnesoma steenstrupii* Koren and Danielssen, 1875.

Diagnosis. — Species small-sized (trunk less than 1 cm in length). Introvert much longer than trunk. Body wall with continuous muscle layers. Oral disk carrying tentacles (less than 10) arranged around mouth but tentacles may be reduced in size or entirely absent. Introvert retractor muscle system highly modified by complete fusion to form single retractor muscle. Anus situated on distal half of introvert. Contractile vessel rarely apparent and without villi. Spindle muscle apparently absent. One nephridium.

Morphological Characters

The following are comments on four troublesome characters used in the descriptions of *Onchnesoma* species.

1. *Introvert length and position of anus.* — The introvert in these species is always longer than the trunk, sometimes several times this length. To measure accurately this structure should be completely extended, but this is rarely the case in preserved material. Measurements made on fully or partially contracted introverts can give deceptively short values. Likewise, when attempting to locate the anus, it is difficult to measure accurately its position unless the introvert is fully extended. In *O. steenstrupii* the anus is 90–95% of the distance towards the mouth, while in others it is 70–85%.

2. *Introvert retractor muscle origin.* — In all these species, the retractor is long and appears as a single muscle (probably due to fusion during its ontogeny) which originates from the posterior tip of the body. Whether there is complete fusion so that there is a single origin (root) or incomplete fusion so that there are two origins is sometimes important. To determine this, one must dissect the posterior end of the trunk, being careful not mechanically to cause a split to occur in an otherwise undivided muscle. The division between the two roots is much easier to see if the introvert (and retractor muscle) is extended.

3. *Tentacles.* — The small tentacles in all species except *O. steenstrupii* can be more easily seen if the introvert is completely extended. Otherwise, one must attempt to open the introvert at the appropriate location. This is an extremely difficult task on such a small diameter cylinder. Care must be taken to not mistake torn tissue for tentacles.

4. *Papillae.* — The presence, size and distribution of these epidermal structures is one of the most easily seen characters and therefore, one useful as an aid in identification. There are distinct differences between taxa but there is also some variation within and between populations of the same taxon.

In *O. steenstrupii* the papillae are small (12–18 μm diameter) and arranged in

rows radiating out from the posterior end forming the “keels” of earlier authors (Fig. 10E). In the subspecies *O. steenstrupii nudum* these keels remain but are folds in the skin, not papillae (Fig. 10D). Similar non-papillated keels exist in *O. magnibathum* (Fig. 10A) and the posterior may occasionally be strongly contracted accentuating these ridges (Fig. 10B). *Onchnesoma squamatum* is uniformly covered with large irregular papillae 80–120 μm in diameter (Fig. 10C). In the subspecies *O. squamatum oligopapillosum* these papillae are smaller and more scattered. The variation within this species is great and abrasion during collection or subsequent washing and sorting may result in the removal of some of these structures. *Onchnesoma intermedium* has ridges posteriorly but bears large papillae similar to *O. squamatum* on the remainder of the trunk.

In general, these papillae and keels are helpful in the identification process, but must be used in conjunction with the entire suite of characters to avoid mistakes.

Key to the *Onchnesoma* Species and Subspecies

1. Trunk with papillae 2
 - Trunk with no papillae but with radiating folds of skin (keels) on posterior end 5
2. Posterior of trunk with well-defined radiating ridges or keels 3
 - Posterior of trunk without well-defined radiating ridges or keels 4
3. Trunk with large papillae on anterior but not posterior and tentacles present *O. intermedium*
 - Trunk with papillae on posterior, sometimes anterior; oral disk instead of tentacles *O. steenstrupii steenstrupii*
4. Trunk covered with many large papillae *O. squamatum squamatum*
 - Trunk with few, small, scattered papillae (may be absent in posterior or mid-trunk) *O. squamatum oligopapillosum*
5. Trunk cylindrical, tapering gradually into narrower introvert ($\frac{1}{2}$ – $\frac{1}{3}$ trunk width); introvert not more than 2 times trunk length; found at depths greater than 2500 m *O. magnibathum*
 - Spherical with abrupt transition to very thin introvert ($\frac{1}{5}$ – $\frac{1}{10}$ trunk width); introvert greater than 4 times trunk length; found at depths less than 1000 m *O. steenstrupii nudum*

Onchnesoma: Systematic Section

Onchnesoma intermedium Murina, 1976

Onchnesoma intermedium Murina, 1976:63–64, fig. 2.

Material examined.—ZIAS—Murina’s co-types.

This species is based on a collection of six specimens. It is reported to have 6–8 tentacles, similar to *O. squamatum*, but differs from it in that the papillae are only distributed over the anterior half to two-thirds of the trunk (not all over). The location of the anus in the mid-region of the introvert (not $\frac{3}{4}$ of the way to the tip) was determined on incompletely expanded introverts. On the co-types we examined, it was very difficult to determine the position of the distal end of the introvert; however, on one specimen the anus appeared to be at least 80% of the distance to the distal end. The non-papillated posterior region of the trunk

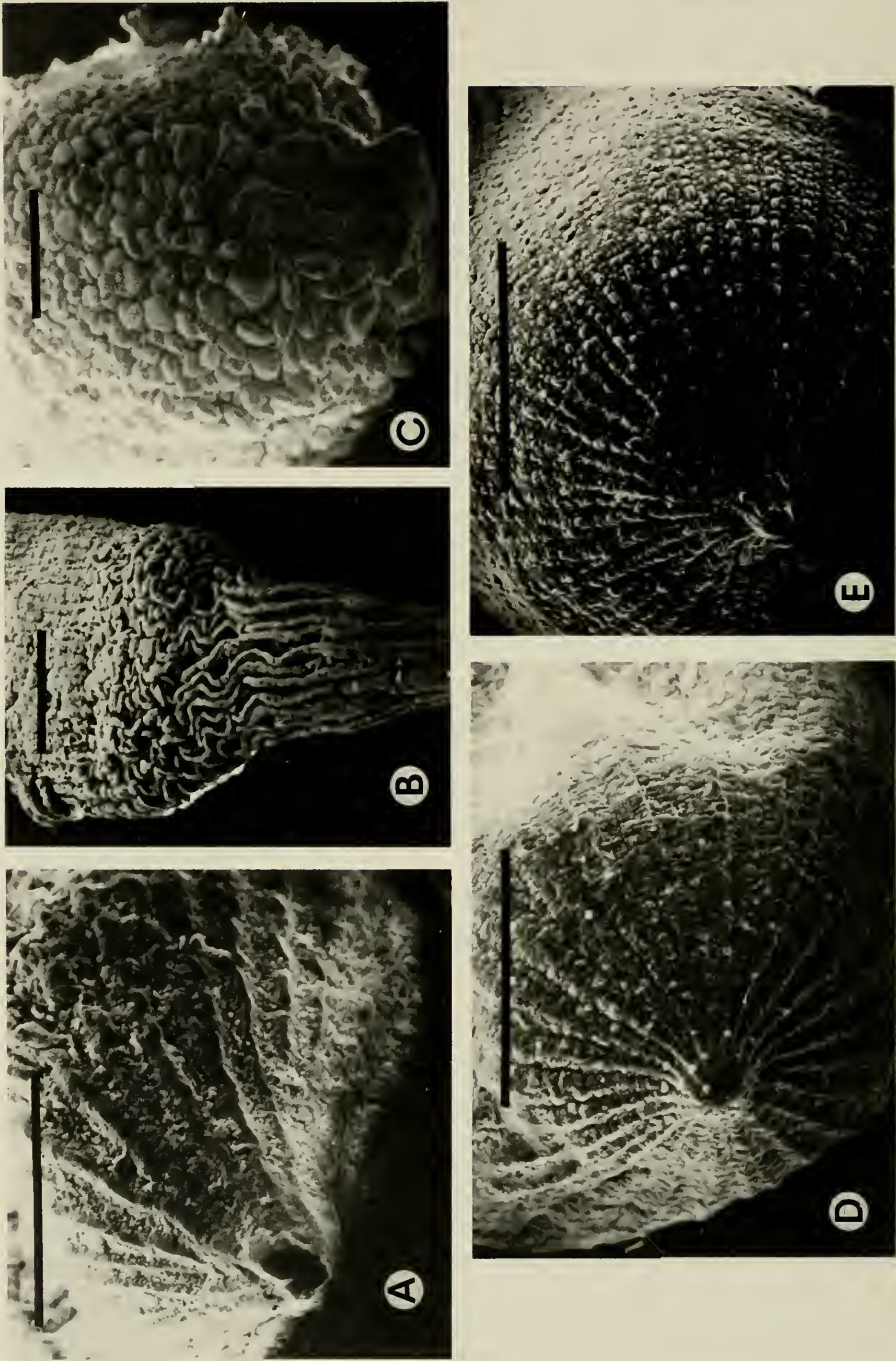


Fig. 10. Scanning electron micrographs of posterior of four *Onchnesoma* taxa: A, B, *O. magnibathum* in two different states of contraction; C, *O. squamatum*; D, *O. steenstrupii* with keels of skin-folds but no papillae; E, *O. steenstrupii* with keels of separate wart-like papillae. (Scale lines = 0.5 mm.)

has longitudinal ridges and furrows. This taxon is not based on a solid foundation and may represent a subset of *O. squamatum*. For the present its separate status is retained but with reservations.

Known distribution.—East China Sea at 500 m.

Onchnesoma magnibathum Cutler, 1969

Onchnesoma magnibatha Cutler, 1969:71–76; 1973:167–168.—Cutler and Cutler, 1980a:454; 1980b:204–205.—Murina, 1973:70.

Onchnesoma steenstrupii.—sensu Murina, 1968b:198.

Material examined.—USNM—type; many recently collected specimens from the North Atlantic.

This deep water species is now well known from the Atlantic Ocean. It is cylindrical, pointed at the posterior end with radiating keels. The introvert is about two times the trunk length and the anus is 70–80% of the distance out towards the mouth. The retractor column has two short origins.

Known distribution.—This is largely an Atlantic Ocean species with one record from the Peru-Chile Trench in the Southeastern Pacific. Generally it lives at depths between 3000–5000 m with a few records as shallow as 2300 m.

Onchnesoma squamatum squamatum (Koren and Danielssen, 1875)

Phascolosoma squamatum Koren and Danielssen, 1875:129; 1877:130–131, pl. 14, figs. 11, 14–15.

Onchnesoma squamatum Stephen and Edmonds, 1972:163 (see this for records and synonymy before 1970).—Cutler, 1973:166–167.—Gibbs, 1977:24–25.

Material examined.—ZMUB—Type-material; many recently collected specimens from the North Atlantic Ocean.

This is a well established North Atlantic species. It has the typical ball-on-a-string appearance, the trunk is covered with papillae, and the anus is 70–80% of the distance toward the mouth. The retractor column has two origins at the posterior end of the trunk and possesses tentacles. See Stephen and Edmonds (1972), Cutler (1973), or Gibbs (1977) for a complete description. One recent collection (27°45'N, 14°13'W, 1934 m) is unique in that the trunks are cylindrical to spindle shaped, not spherical as is common, and they gradually taper into the narrower introvert unlike the ball-on-a-string appearance. The body wall is covered with irregular evenly distributed golden tan papillae somewhat less dense than in the northern population.

Known distribution.—This species appears restricted to the North Atlantic and Mediterranean Sea generally from depths of 150–1400 m. On the eastern side it has been reported from the Canary Islands (27°N) to Iceland (63°N), while on the western side it is found from Florida to North Carolina (24–34°N). The Mediterranean records are very shallow (10–55 m; Murina 1964a)

Onchnesoma squamatum oligopapillosum Cutler, Cutler, and Nishikawa, 1984

Onchnesoma squamatum oligopapillosum Cutler et al., 1984:281–282.

Material examined.—USNM—type-material.

This Japanese population is the only Pacific Ocean record of this taxon. It differs from the nominate form by having fewer, smaller, scattered papillae.

Known distribution.—Pacific side of Honshu, Japan, 14–250 m.

Onchnesoma steenstrupii steenstrupii Koren and Danielssen, 1875

Onchnesoma steenstrupii Koren and Danielssen, 1875:133; 1877:142, pl. 15, figs. 28–36.—Stephen and Cutler, 1969:118.—Murina, 1971:82; 1972:304–305; 1978:124.—Stephen and Edmonds, 1972:163–164 (see this for records and synonymy before 1969).—Cutler, 1980b:205–206.—Zavodnik and Murina, 1975:128.

Phascolion dogieli Murina, 1964a:70–71.—Stephen and Edmonds, 1972:176.

Material examined.—ZMUB—Type-material; recently collected specimens from the North Atlantic Ocean.

This is a well established and common species. It is spherical with a very long introvert at the end of which is an oral disk, not tentacles. The anus is 90–98% of the distance toward the mouth. It has radiating keels on the posterior end and completely fused retractor column. See Stephen and Edmonds (1972), Cutler (1973), or Gibbs (1977) for a complete description.

Known distribution.—In general this species inhabits cool to cold waters at bathyal depths on continental slopes. It is common in the North Atlantic but present in the Southeastern Atlantic, higher latitudes of the Western Pacific and the Southwestern Indian Ocean. There are very few records from depths less than 100 m or greater than 1600 m. Reports that seem atypical include the Mediterranean at 40 m (Zavodnik and Murina 1975), and three very deep (2135–2988 m) unpublished records in the eastern Atlantic Ocean (Cutler and Cutler, in prep.).

Onchnesoma steenstrupii nudum, new subspecies

Material examined.—273 specimens from H. Sanders, cruise 42 of Atlantis II to Walvis Bay/Luanda; Sta 185–190 at 22°56' to 23°05'S and 12°45' to 13°05'E, 16–17 May 1968.

This group of worms from this restricted geographical region in the Southeastern Atlantic Ocean forms a distinctive population. The morphological distinction from the nominate form is the nature of the epidermis. When viewed under the dissecting microscope the epidermis has a unique ridged appearance. However, microscopic examination of skin mounted in glycerine reveals that the ridges are not made up of scales, papillae or plates as in other *Onchnesoma*. When transverse sections of the body wall are made, it appears to be only small folds or wrinkles in the epidermis giving this effect. Scanning electron micrographs corroborate this (Fig. 10D).

The introvert is at least 5–6 times the trunk length (trunks 0.5–2.0 mm) and terminates in a modified tentacular apparatus reduced to a disk as in *O. steenstrupii*. However, there is one specimen that has about six subdivisions or tentacular lobes. Internally the retractor muscles are completely fused with a single origin at the posterior tip of the trunk. The single nephridium is about $\frac{1}{3}$ – $\frac{1}{2}$ the trunk length, unattached and on the right side at the anterior end of the trunk. The gut has a regular spiral and is attached by three fixing muscles to the body

wall. The anus is located 90–95% of the distance toward the distal end of the introvert.

The name of this new subspecies reflects the absence of radiating, scale-like papillae on the posterior of the trunk which characterize the nominate form. The epidermal ridges which replace these papillated rows make this taxon easily recognizable. The general shape, size, and internal organization are comparable. This apparently restricted range (around 23°S and 13°E with a vertical range of 460–1011 m) may be unreal. *Onchnesoma steenstrupii steenstrupii* is found in nearby but deeper water (2100–2500 m).

The holotype from St. 188 is deposited in the National Museum of Natural History, Washington, D.C., USNM 081987; the paratypes from the same station are USNM 081988.

Discussion

Our analysis shows one major evolutionary trend within this pair of genera (fusion of introvert retractor muscles) sometimes paralleling other changes. The least derived form is exhibited by the *P. tuberculosum* group having two muscles (a dorsal and a ventral) of equal size, separated for most of their length. From this morph two lines are evident. One leads to the *P. strombus* condition, i.e., a marked reduction in the relative size of the ventral muscle. The second involves the fusion of dorsal and ventral muscles going through the *P. pacificum* morph (partial) to the *P. cryptum* and *Onchnesoma* morph of a single retractor column.

The tentacular crown has also undergone two basic changes. The primitive state is 15–25, well-developed tentacles (*P. strombus*). From this, one trend is toward a reduction to a few lobes or only an oral disc as in *O. steenstrupii*. A second (rare) trend is toward an increasing number (more than 35), thinner, elongate tentacles (*P. medusae*).

A third character of interest is hooks. There are three evident trends away from the common thin, pointed spine-like form (Type I). One group of species developed a more massive, recurved structure (Type II), a second group developed small hooks with rounded tips and a more circular base (Type III). There is a fourth group of eight species which appears to have no hooks.

The zoogeographical picture that we have of the species in these genera is not presented in detail here. We have a large number of unpublished records from several parts of the world's oceans which contain *Phascolion* and *Onchnesoma* species and we believe it premature to make a detailed statement. However, there are a few interesting generalizations one can make:

1. *P. strombus* is very widely distributed in cool water from shelf and slope depths generally at latitudes higher than 30°N and S.

2. As a group, these genera seem adapted for cool or cold water but are largely absent from abyssal depths and lower latitudes at shallow depths except in upwelling regions off West Africa. When species are present in non-upwelling areas and shallow water (*P. cryptum*, *P. cirratum*, *P. robertsoni*) they appear to be very localized. The one exclusively abyssal species (*O. magnibathum*) is widely distributed in the Atlantic Ocean only.

3. Between *P. strombus* and those with very localized distributions, there are

Table 1.—Species considered with summary of proposed taxonomic changes.

Present name	Proposed name
<i>Phascolion abnorme</i> Fischer, 1895	no change
<i>Phascolion africanum</i> Fischer, 1923	<i>Phascolion strombus</i>
<i>Phascolion alberti</i> Sluiter, 1900	<i>Phascolion strombus</i>
<i>Phascolion anomalus</i> Murina, 1981	<i>Phascolion strombus</i>
<i>Phascolion artificiosum</i> Ikeda, 1904	<i>Phascolion strombus</i>
<i>Phascolion beklemischevi</i> Murina, 1964	<i>Phascolion convestitum</i>
<i>Phascolion bogorovi</i> Murina, 1973	no change
<i>Phascolion botulus</i> Selenka, 1885	incertae sedis
<i>Phascolion brotzkajae</i> Murina, 1964	<i>Phascolion strombus</i>
<i>Phascolion canum</i> Cutler and Cutler, 1980	<i>Phascolion lutense</i>
<i>Phascolion caupo</i> Hendrix, 1975	no change
<i>Phascolion cirratum</i> Murina, 1968	no change
<i>Phascolion collare</i> Selenka et al., 1883	no change
<i>Phascolion convestitum</i> Sluiter, 1902	no change
<i>Phascolion cronullae</i> Edmonds, 1980	<i>P. strombus cronullae</i>
<i>Phascolion cryptum</i> Hendrix, 1975	no change
<i>Phascolion dentalicolum</i> Sato, 1937	<i>Phascolion hedraeum</i>
<i>Phascolion dogieli</i> Murina, 1964	<i>Onchnesoma steenstrupii</i>
<i>Phascolion hedraeum</i> Selenka et al., 1883	no change
<i>Phascolion heteropapillosum</i> Wesenberg-Lund, 1963	<i>Phascolion abnorme</i>
<i>Phascolion hibridus</i> Murina, 1981	no change
<i>Phascolion hironellei</i> Sluiter, 1900	<i>Phascolion tuberculosis</i>
<i>Phascolion hupferi</i> Fischer, 1895	no change
<i>Phascolion ikedai</i> Sato, 1930	species inquirendum
<i>Phascolion indicus</i> Murina, 1974	<i>Phascolion hupferi</i>
<i>Phascolion kurchatovi</i> Murina, 1974	<i>Phascolion hedraeum</i>
<i>Phascolion lucifugax</i> Selenka et al., 1883	no change
<i>Phascolion lutense</i> Selenka, 1885	no change
<i>Phascolion manceps</i> Selenka et al., 1883	incertae sedis
<i>Phascolion mediterraneaum</i> Fischer, 1922	<i>Phascolion convestitum</i>
<i>Phascolion medusae</i> Cutler and Cutler, 1980	no change
<i>Phascolion megaethi</i> Cutler and Cutler, 1979	no change
<i>Phascolion microspheroidis</i> Cutler and Duffy, 1972	no change
<i>Phascolion moskalevi</i> Murina, 1964	species inquirendum
<i>Phascolion murrayi</i> Stephen, 1941	<i>P. valdiviae sumatrense</i>
<i>Phascolion pacificum</i> Murina, 1957	no change
<i>Phascolion pallidum</i> Koren and Dan., 1877	<i>Phascolion tuberculosis</i>
<i>Phascolion parvum</i> Sluiter, 1902	species inquirendum
<i>Phascolion pharetratum</i> Sluiter, 1902	no change
<i>Phascolion rectum</i> Ikeda, 1904	no change
<i>Phascolion robertsoni</i> Stephen and Robertson, 1952	no change
<i>Phascolion sandvichi</i> Murina, 1974	species inquirendum
<i>Phascolion strombus</i> Montagu, 1804	no change
<i>Phascolion sumatrense</i> Fischer, 1916	<i>P. valdiviae sumatrense</i>
<i>Phascolion temporariae</i> Edmonds, 1976	<i>Phascolion tuberculosis</i>
<i>Phascolion tortum</i> Edmonds, 1976	<i>Phascolion strombus</i>
<i>Phascolion tridens</i> Selenka et al., 1883	<i>Phascolion collare</i>
<i>Phascolion tuberculosis</i> Theel, 1875	no change
<i>Phascolion tubicolum</i> Verrill, 1873	<i>Phascolion strombus</i>
<i>Phascolion ushakovi</i> Murina, 1974	no change
<i>Phascolion valdiviae</i> Fischer, 1916	no change
<i>Onchnesoma intermedium</i> Murina, 1976	no change
<i>Onchnesoma magnibatha</i> Cutler, 1969	no change
<i>Onchnesoma squamatum</i> Koren and Dan., 1875	no change
<i>Onchnesoma steenstrupii</i> Koren and Dan., 1875	no change

only four species of *Phascolion* (*tuberculosis*, *hedraeum*, *lutense*, *pacificum*) recorded from wide areas. These four species are also taxa with non-specialized morphological character states. In *Onchnesoma* three of the four species are distributed over a fairly broad range.

4. The Eastern Pacific Ocean and the coasts of India seem to lack representatives of these genera.

5. Being common in the Arctic and Antarctic Oceans makes *Phascolion* a subject of interest in discussions of bipolarity.

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